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THE PEG OF THE CUCURBITACEAE

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(WITH SIX FIGURES)

Historical

The peg of seedling Cucurbitaceae has frequently been used as a marked case of adaptation to a peculiar function. It holds the seed coat while the elongating arms of the arch of the hypocotyl

FIG. 1.—Big Tom, showing the pegs functioning in the removal of the coats.

withdraw the cotyledons from the coat. The method by which the peg functions is well shown in fig. 1.

MIRBEL[1] and TITTMAN[2] very early showed the presence of this organ throughout the Cucurbitaceae. While it is well developed in the epigean forms, it is very rudimentary in the hypogean forms, such as *Megarhiza californica* and *Sicyosperma gracilis*. The organ is by no means limited to the Cucurbitaceae, but appears in various genera of a number of families: *Mirabilis*, *Oxybaphus*, and *Abronia* (Nyctaginaceae), *Martynia* (Martyniaceae), *Lindheimera* (Compositae), *Mimosa* (Leguminosae), *Tribulus* (Zygophyllaceae), *Eucalyptus* (Myrtaceae), *Cuphea* (Lythraceae), etc. While in Cucurbitaceae the peg appears only after germination has progressed considerably, in other forms, as *Eucalyptus* and *Cuphea*, it is already laid down as a complete ring in the mature seed, and with germination completes its development.

TITTMAN recognized the biological significance of this organ in the Cucurbitaceae, and showed that it appears only on the lower side of the developing hypocotyl.

TSCHERNING[3] gives a rather full description of its histology and physiology. He states that it is a parenchymatous outgrowth. While the greater diameter of the parenchymatous cells in other parts of the hypocotyl is longitudinal, in the peg zone it is radial. The number of layers of cortical cells is also somewhat greater at the peg zone. TSCHERNING describes the effect of the position of the seed during germination upon the development and functioning of the peg. He says that when the radicle points vertically downward the swelling does not occur, and the cotyledons push above the ground still bearing the coat. With radicle pointing vertically upward, the peg develops on the concave side of the arch, but does not remove the coat. When the seeds are planted on edge, the peg develops on the concave side of the arch and wedges between the two valves of the coat, thus succeeding in removing a considerable percentage of them. When the seeds are planted on a flat face, the peg develops on the concave side of the arch and attaches itself securely to the lower valve of the coat, thereby insuring its removal. TSCHERNING emphasizes the development of the peg on the concave side of the arch, and speaks of it as a lateral pushing out of the cells due to the inhibition in the

[1, 2, 3] See under NOLL, footnote 8.

elongation on the concave side of the hypocotyl. While his relating its place of development entirely to the arch is probably correct, as we shall see later, his view as to how the arch brings about such a placement is crude. We shall see also that his claim that the peg does not develop when the seed grows with the radicle pointing vertically downward is incorrect.

FLAHAULT[4] claimed that seedlings that developed when the removal of the coats occurred in the normal way were far superior to those in which it was prevented by breaking away a portion of the lower valve of the coat so that the foot could not get a hold. This advantage he attributes of course to the hindering of assimilation by the retained coats. He claimed that the peg develops at any point on the hypocotyl necessary to enable it to hold the coat.

CHARLES DARWIN,[5] contrary to FLAHAULT, found that the peg develops only at the zone between root and stem. The lower face is root, as shown by the presence of root hairs and reaction to potassium permanganate, while the upper face is stem. DARWIN described a number of experiments, similar to those of TSCHERNING, testing the effect of the position of the seed upon the development and functioning of the peg. While DARWIN clearly showed that the peg is located at the border between root and stem, he did not show the stimuli involved in its lateral placement.

FRANCIS DARWIN[6] later showed that seedlings of *Cucurbita ovifera*, allowed to germinate on a slowly rotating clinostat with a horizontal axis, gave pegs completely surrounding the hypocotyl and approximately equal on all faces. He concluded, from the inadequate experiments of his father and himself, that gravity is a direct stimulus determining the lateral distribution of the peg, and that therefore this experiment shows that gravity is continually effective on the clinostat and only equalized in its action on the several flanks of the exposed object. The conclusion concerning

[4] FLAHAULT, C., Sur le talon de la tigelle de quelques Dicotylédones. Bull. Soc. France **24**: 200. 1877.

[5] DARWIN, CHARLES and FRANCIS, The power of movement in plants. pp. 102–107. New York. 1892.

[6] DARWIN, F., and ACTON, E. H., Practical physiology of plants. pp. 192 ff. Cambridge. 1895.

the nature of the effect of the clinostat is correct, as shown by FITTING[7] and others, but the assumption that this experiment proves it is quite another question, and, as we shall show later, quite out of accord with a number of other facts.

NOLL[8] mentioned the fact that FRANCIS DARWIN'S conclusion that gravity is a direct stimulus in determining the lateral distribution of the peg is not proved by his meager experiments. He also claimed that only 50 per cent or less of the seedlings grown on a clinostat produce ringlike pegs, while the remainder show sharp arching, with a one-sided peg. NOLL stated that all flanks of the hypocotyl are qualitatively equally capable of peg-development, but that quantitatively the broader flanks produce the larger peg. He concluded that contact of the seed coats is not a necessary stimulus to peg-development, for the peg still appears when the coats are removed. The contact of the coat, however, increases the size of the peg. He performed a number of experiments in which seeds were germinated with the two opposite broad faces exposed to gravity alternately and for equal periods. In all these cases the two faces developed essentially equal pegs. He especially emphasized these as showing that the peg stands in strong relation to gravity and owes its stimulus for formation to gravity. Many experiments were also performed in which seedlings were grown with the radicle directed perpendicularly downward or at a slight deviation from this position. From these he concluded that the gravity stimulus reaches beyond the lower pole of the seedling axis. At a deviation of 5° from the vertical he found a weak peg on the upper side, while at 7°5 the peg was almost exclusively on the lower side. He fixed the limit of the field of stimulation at 6°–8° deviation from the vertical. He specified that these are to be taken only as approximate figures and as applying to *Cucurbita Pepo*. In two seedlings slight pegs were found on the upper side at a deviation of 8°. Seedlings were also found that showed no peg, but he did not know how to account for this. On account of great variation in response, NOLL empha-

[7] FITTING, HANS, Jahrb. Wiss. Bot. **45**:575–600. 1909.

[8] NOLL, F., Zur Keimungs-Physiologie der Cucurbitaceen. Landwirt. Jahrb. **30**:145–165. 1901.

sized that reliable conclusions can be drawn only by the employment of a large number of seedlings in each culture.

It is evident that both FRANCIS DARWIN and NOLL considered gravity as well as the arching of the hypocotyl as direct stimuli in determining the lateral distribution of the peg. NOLL says (p. 164): "Die meiste inseitige Ausbildung des Wulstes tritt als Ergebnis zweier heterogener Reize ein. Die localisierte Entstehung des Wulstes ist einerseits abhängig vom Gravitationsreiz. Der Wulst bildet sich auf der jeweiligen Unterseite. . . . . Die einseitige Wulstbildung wird andererseits auch bedingt durch die Krummung des Mutterorgans, derart, dass auf der Konkavseite die Bildung des Stemmorgans ausgelöst wird."

FRANCIS DARWIN[9] has lately used the peg of the cucurbits as a mainstay for the memory theory of plant response. In this, of course, he assumed that its development and position are directly determined by gravity. Whether gravity acts as a direct stimulus to its production and placement is the principal question to be tested by the following experiments.

Methods and materials

NOLL failed to control the factors involved in this problem in a way that enabled him to determine the part played by each in the lateral placement of the peg. He apparently failed to notice the potency of contact of the coats on the one hand, and of the media on the other, in arch-production. In the experiments here given, to avoid this important influence, except when its effect was to be studied, the seeds, whether on the clinostat, centrifuge, or in rest positions of different inclinations, were freed from the coats at the tips and each held by two pieces of cork between which the cotyledons were clasped at the central region. The whole apparatus was kept in the dark and watered by a very fine spray heated to 23° C. The spray was formed by forcing the water by means of tap pressure through a tank of considerable size kept in a water bath at constant temperature, and allowing it to break against a plate of glass. In this way contact of both the coats and the soil media is entirely eliminated. Contact, as data later given will

[9] DARWIN, FRANCIS, New Phytologist **5**:199–207. 1906.

show, is a very important influence. We are unable to see how NOLL could get results at all dependable without taking this precaution. He was always studying the effect of two stimuli when his results purport to be considering one.

The seeds used in this work were obtained from VAUGHAN and will be mentioned by the trade name used by that dealer.

Experiments and discussion

EFFECT OF CONTACT OF COATS

As has been stated, the contact of coats plays a very important part in arch-production, and therefore indirectly upon the lateral

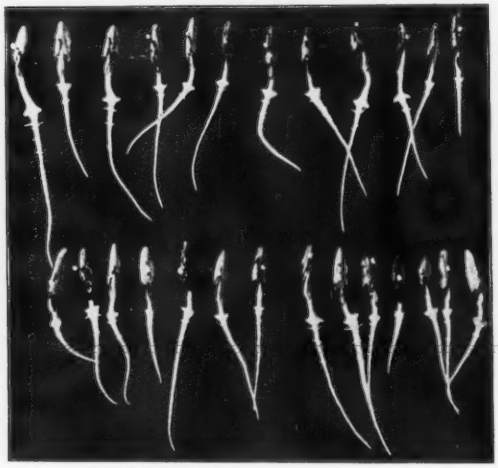

FIG. 2.—Crop of Hubbard squash grown in spray at 23° C.; coats removed at the tip and radicles pointing downward.

placement of the peg. This effect was tested in two ways: (1) by growing seeds upon a clinostat with coats intact and with coats removed at tips, and (2) by a similar growth of seeds held between cork strips with radicles pointing downward or approximately so. These were kept in a dark chamber and watered with a spray at 23° C., as described above. There is some variation in different varieties in the response to contact. For example, the pump-

kin called Big Tom, especially when grown on the clinostat, gives a somewhat higher percentage of strong arching in response to coat contact than does the Hubbard squash. Fig. 2 shows all the individuals of a culture of Hubbard squash grown as described above, coats removed at tip, and radicles pointing downward. Of the 26 seedlings, none are sharply arched, and all have pegs either two-sided or ringlike. Three show slightly more prominent pegs on one side than on the other. It is evident then that in

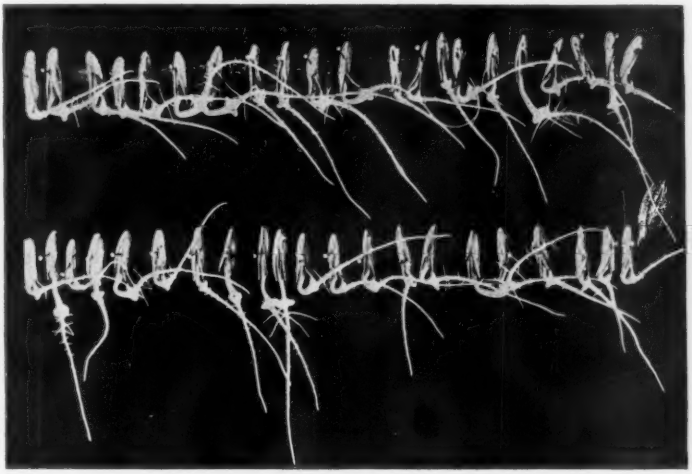

FIG. 3.—Crop of Hubbard squash as in fig. 2, but coats not removed at tip; shows sharp arching induced by contact of coats.

the Hubbard squash little arching and no one-sided pegs are produced if the seedlings grow with the radicles pointing vertically downward, and with no contact of either coat or media. Fig. 3 shows a similar culture except that the coats were intact during the growth. Of the 42 seedlings, 29 are sharply arched and 13 very slightly or not at all. This shows contact of coats to be very potent in arch-production. Of those that are sharply arched, 8 have pegs entirely on the concave side of the arch, while several others show the greater peg-development on that side. In this case the arching is against gravity, which emphasizes the potency of con-

tact of coats as a stimulus to arching. By a comparison of figs. 2 and 3, one can see clearly the effect of contact upon the size of the peg.

A culture of pumpkin (Big Tom), with coats removed, radicles pointing vertically downward, and grown in a spray as described above, produced 39 seedlings. Of these none were sharply arched; 19 showed very small two-sided pegs; 19 were essentially pegless; and 1 showed a small one-sided peg on the concave side of the slight arch. A similar culture of the pumpkin (Big Tom) with coats intact gave 31 seedlings; of these, 25 were sharply arched, with pegs entirely on the concave side of the arch; 1 was little arched, with peg on concave side of arch; 3 were pegless; and 2 had equal, small, two-sided pegs. From these data it is evident that in the pumpkin (Big Tom) contact of coats is even more effective in producing arching than in the squash (Hubbard), and unlike the case of the squash, the arching shifts the peg entirely to the concave side of the arch. From the large number of pegless seedlings appearing in the culture with the coats removed, it is also evident that the arch not only determines the lateral placement of the peg, but in some cases even its appearance. One may be inclined to think the existence of the peg is perhaps determined by the contact of the coat, rather than by the arching produced by the coat; but it is not probable, for of the 6 not arched in the culture with coats on, 3 are pegless. It is apparent, therefore, that a large number of the pumpkins (Big Tom) are pegless if developed without considerable arching, and that arching determines in about half the cases whether or not there will be a peg, as well as the placement of the peg on the concave side of the arch.

Fig. 4 shows a culture of pumpkin (Big Tom) with coats removed at the tips, and grown on the horizontal clinostat in a spray. Of the 30 seedlings in the culture, none are sharply arched; 14 have small two-sided pegs; 8 show slight pegs on the concave side of the slight arch; and 8 are essentially pegless. Fig. 5 shows a similar culture except the coats are intact. Of the 24 seedlings, 20 are sharply arched, with pegs entirely on the concave side of the arch; 2 are slightly arched, one of which has an equal two-sided peg and the other a slight one on the concave side of the arch;

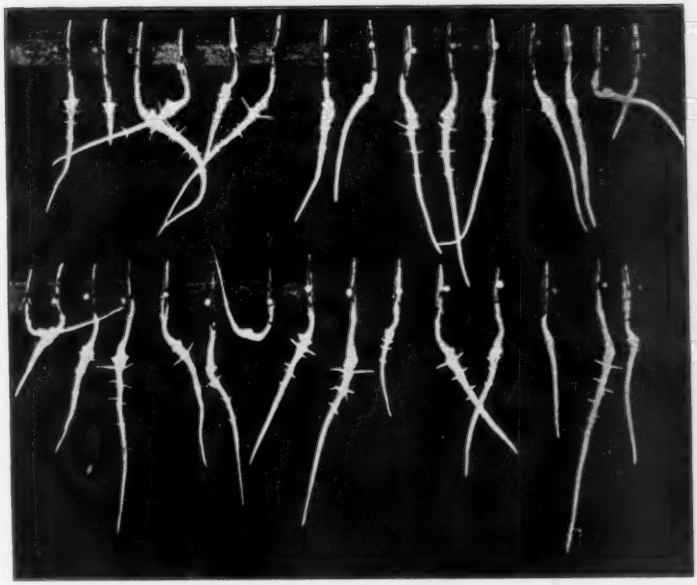

FIG. 4.—Crop of Big Tom grown on a clinostat in a spray; temp. 23°; coats removed at the tip.

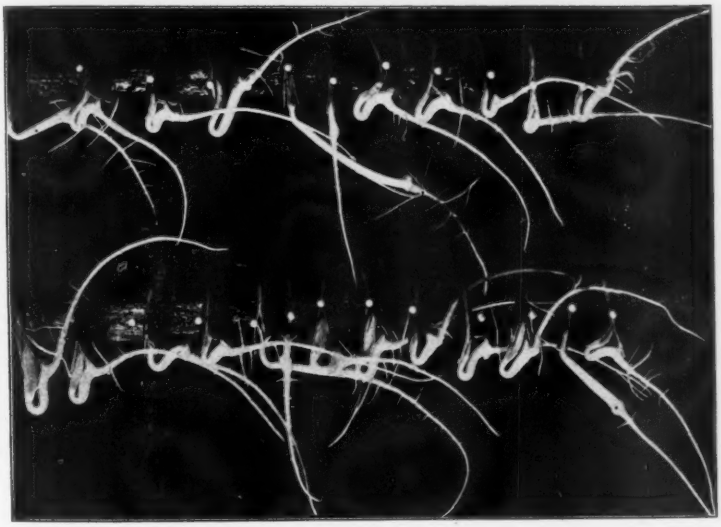

FIG. 5.—Crop of Big Tom grown as fig. 4, except coats were not removed at the tip.

2 show no arch and are essentially pegless. One is struck here by the small percentage of pegless seedlings in the culture in which the coats are removed, as compared with corresponding seedlings grown with the radicle pointing vertically downward. This is easily explained, however; the arching does not have to take place against gravity, due to the equalization of this stimulus by the clinostat. In short, the autonomic disposition to arch is unrestrained. This fact, with the fact that slight arching produces a one-sided peg in this form, makes the data exactly what must be expected. Again, one sees that the contact of the coats is much more effective in producing arching and one-sided peg-development than in the culture in which the seedlings developed with the radicle pointing vertically downward. This again must be expected, for the arching does not have to occur in opposition to gravity, since this stimulus is equalized by the clinostat.

NOLL states that more than 50 per cent of pumpkins grown on a horizontal clinostat show sharp arching, with the peg entirely on the concave side of the arch. This is the case if one allows two factors to act at once: contact of coats and the autonomic tendency to arch. But NOLL'S conclusion that such results will follow from the autonomic tendency to arch alone is erroneous, and was possible only because he overlooked the very important influence of contact of coats in the arching. DARWIN'S statement that in seedlings of *Cucurbita ovifera*, grown on the clinostat, the peg is almost equal on all sides, certainly holds for the squash (Hubbard), providing both contact of coats and media are avoided, as they were in our clinostat cultures.

From the experiments stated in this section several things are evident. Contact of coats is an extremely important stimulus for arch-production, both in the pumpkin and the squash. It produces strong arching even against gravity. In the pumpkin (Big Tom) any considerable arching increases greatly the percentage of seedlings that show pegs; and it causes the development of the peg on the concave side of the arch. In the squash (Hubbard) arching is far less effective in determining the lateral placement of the peg. The autonomic tendency to arch is very slight, though it tends to a lateral placement of the peg in the pumpkin (Big

Tom), as shown by the clinostat experiments where the coats are removed. It is also evident that results obtained without reference to the effect of contact of the coats cannot lead to a knowledge of the part played by the several factors in determining the lateral placement of the peg.

EFFECT OF DEVIATION FROM THE VERTICAL POSITION

As has been stated, NOLL claimed that seedlings grown in a vertical position, with the radicle pointing downward, gave two-sided or ringlike pegs. He found, however, that a slight deviation from this position (8°.5) produced only one-sided pegs. We ran numerous experiments on various varieties of cucurbits for the purpose of testing this statement. The results are tabulated in the accompanying table. "Vertical" in this table means that the seed was held so that the plane passing through the largest dimension of the seed was in a vertical position and the radicle was pointing downward. Deviations from this plane were made by tilting the plane of the seed the number of degrees from this position that is recorded in the table. The tilting always exposes one face rather than the edge of the seed to gravity. The seeds were held in position by two pieces of cork lightly clasping them at the central region. The whole culture was grown in darkness in a spray, so that no contact of media was involved and no contact of coats except when specified.

A glance at this table makes it very evident that it furnishes no ground for NOLL'S conclusion that a deviation of over 8°.5 gives only one-sided pegs. Our extensive experiments make us unable to understand how he obtained such results.

It is evident from the table that in every variety used the deviation from the vertical is far more effective in the lateral placement of the peg when the coats are intact than when they are removed at the tip. This is due to the fact that the arching is made much sharper by the coat contact, and the lateral placement is in turn furthered by the sharper arching.

It is also noticeable that there is a great variation in the several varieties in the effectiveness of the deviation for the lateral placement of the peg. In Big Tom it is most effective, while in Boston

Deviation from vertical position		Vertical			10°			20°			30°			45°			65°			90°			135°			150°			165°			180°		
Nature of peg		1-sided	2-sided	pegless	1-sided	2-sided	pegless	1-sided	2-sided	pegless	1-sided	2-sided	pegless	1-sided	2-sided	pegless	1-sided	2-sided	pegless	1-sided	2-sided	pegless	1-sided	2-sided	pegless	1-sided	2-sided	pegless	1-sided	2-sided	pegless	1-sided	2-sided	pegless
Variety	Condition of coat at tip																																
Big Tom (pumpkin)	removed	6	27	37	0	4	5	1	6	6	0	11	4	16	27	5	18	6	0	47	19	0	59	0	0	60	0	..	57	0	..	42	0	..
	intact	30	7	1	15	1	0	16	4	1	3	3	..	35	4	0	17	0	0	43	1	0	101	0	1	30	0	..	46	0	..	50	0	..
Hubbard (squash)	removed	5	44	1	0	8	0	3	10	..	..	..	..	22	41	0	..	..	..	38	3	0	38	3	0	..	..	..	..	..	..	..	..	..
	intact	3	23	1	1	10	0	1	12	..	..	..	..	27	17	0	..	..	..	46	2	0	46	2	0	..	..	..	..	..	..	..	..	..
Boston marrow (squash)	removed	..	..	..	..	..	..	22	22	..	1	27	..	0	6	0	5	15	..	..	..	..	19	9	0	24	8	0	54	3	0	58	4	..
	intact	..	..	..	6	29	..	6	42	..	13	11	..	..	..	..	8	4	..	..	..	..	35	2	0	38	5	0	47	4	0	45	1	..
Calhoun (squash)	removed	..	..	..	..	..	..	..	..	..	0	23	..	2	13	0	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
	intact	..	..	..	..	..	..	..	..	..	2	13	..	4	5	0	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Sugar pie (pumpkin)	removed	..	..	..	..	..	..	..	..	..	8	2	7	27	31	4	..	..	..	103	29	12	..	..	..	..	..	..	..	..	..	..	..	..
	intact	..	..	..	..	..	..	..	..	..	9	3	9	23	4	3	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..

marrow it is least so. In the former no two-sided pegs appear at 135° deviation or above, while the latter at 180° deviation still shows about 8 per cent with two-sided pegs.

In the exposures with the coats removed, one can see the effectiveness of gravity alone in the one-sided peg-production. It must not be forgotten that the effect of gravity in lateral placement of the peg is probably entirely indirect and acts through the production of an arch.

As has been mentioned, NOLL thought that not only the development of the peg but its lateral placement is called forth by the joint action of two heterogeneous stimuli: gravity, which causes the development on the lower side of the hypocotyl; and "organform" stimulus, which causes the development on the concave side of the arch. NOLL compared the second of these to the appearance of lateral roots on the convex side of a curved main root. His main evidence for the conclusion concerning two heterogeneous stimuli is based on his experiments in which he grew seedlings at various deviations from the vertical (radicles pointing downward). If his statement that any deviation beyond 8°.5 always produces a one-sided peg were true, his conclusion would be entirely justified. Our results, derived by the use of five different varieties of cucurbits, of very different characters so far as peg-development is concerned, and obtained with greatest care in eliminating all factors, except gravity, show that it takes a deviation of not merely 8°.5, but in every case of more than 90°, and in forms like the Boston marrow of more than 135°, to insure a one-sided peg. When a seedling grows in the horizontal position, gravity and the "organform" stimulus certainly are both acting to produce the peg on the lower side only, and yet our results show that many seedlings thus grown produce two-sided pegs. NOLL'S two heterogeneous stimuli are not adequate to explain these results. This view becomes yet less in accord with fact when it is remembered that NOLL assumed that gravity could not reach more than 8°.5 over the lower pole of the hypocotyl, that is, that gravity is not effective in inducing peg-development on the upper side of the hypocotyl if the deviation from the vertical is over 8°.5.

It has already been pointed out that in *Eucalyptus* and *Cuphea*

a ringlike peg is laid down in the formation of the seed, and with germination this enlarges somewhat. In these forms, therefore, the peg is a natural outgrowth approximately equal on all flanks of the seeds; its appearance and development are related, undoubtedly, to the plant form and not called forth alone by external stimuli. We find that such a ringlike peg, rather small but approximately equal on all flanks, develops on the seedling of palo verde (green-stemmed *Parkinsonia*). In this form the arching of the hypocotyl is not marked and the peg does not function in the removal of the coat; likewise, external conditions do not seem to lead to a lateral placement. Results already stated, as well as data to be stated later, lead us to believe that the peg of the cucurbits is, to a considerable degree, a natural outgrowth of the seedling, and that it is approximately equal on all flanks if arching is avoided. We must of course accept the quantitative greater development on the two broader faces of the hypocotyl over the two narrower. It is also evident that in different species the size of the outgrowth varies greatly; it is relatively large in squashes (Hubbard, Boston marrow, and Calhoun), and relatively small or even absent in pumpkins (Big Tom and Sugar pie). We have also found the latter to be the case in various watermelons and cucumbers. In fact, if arching is avoided, different species will show all the intermediate forms from the so-called pegless (fig. 6) to those that have very prominent ringlike pegs. We must also recognize that the contact of coats, as figs. 2 and 3 show, greatly increases the size of this outgrowth. The size is also greatly increased, at least on one flank, by arching.

FIG. 6.—Pegless seedlings of Big Tom.

The question, therefore, does not seem to be so much what stimuli cause the development of this organ, as DARWIN and NOLL assumed, but rather what stimuli lead to its lateral placement and tend to increase its size.

It is certainly evident, as all who have worked on this subject agree, that arching or "organ-form" stimulus, as NOLL termed it, leads to the shifting of the peg to the concave side of the hypocotyl, or, as it would be better termed, to the development of the peg on the concave flank of the hypocotyl. Both gravity and contact of coats aid in arch-production. Of these, as our results show, the latter is much more important. Contact of coats also greatly increases the size of the peg. Other questions that should be answered in this connection are whether or not gravity acts as a direct stimulus in the lateral placement of the peg, and whether or not it tends to increase the size of the peg on the flank exposed to it.

As has been repeatedly said, both DARWIN and NOLL assumed that gravity is a direct stimulus, not only in determining the existence of a peg but also its lateral placement. DARWIN'S evidence for this was that a ringlike peg is found when the seedlings of *Cucurbita ovifera* were grown in a horizontal position on a slowly rotating clinostat. NOLL'S evidence for this conclusion included two other facts: (1) seedlings with the radicle pointing downward but deviated more than 8°.5 from the vertical gave pegs only on the lower side, and (2) seedlings turned over every few hours during development gave pegs ringlike or two-sided. We have shown that NOLL'S deviation experiments do not at all accord with results obtained with all care to avoid the variation of more than one factor at a time. As for the clinostat and turning evidence, it is just what would be expected if the peg is an outgrowth approximately equal on all sides, if sharp arching is avoided. Of course the clinostat and the turning from time to time prevent sharp arching, and thereby give the natural ringlike or two-sided development.

Further evidence as to whether gravity is a direct stimulus in determining the existence of a peg, its lateral placement, or its size, is found in the sections that follow.

CENTRIFUGE CULTURES

A large number of cultures of the several varieties of cucurbits worked with were made on a centrifuge with a vertical axis. The acceleration varied from two gravities to eighteen gravities. The

cultures were grown in a spray at 23° C.; the coats were removed to avoid all contact; and the long axis of each seed was arranged parallel with a radius of the centrifuge, the radicle directed away from the axis.

Three facts were noticeable in such seedlings, especially in those grown with the greater centrifugal acceleration: (1) the hypocotyls were very straight, (2) the pegs were smaller than in similar cultures on clinostat or with radicles pointing vertically downward, and (3) the pegs though small were approximately equal on all flanks.

If, as NOLL assumes, gravity calls forth the peg in seedlings with the radicles pointing downward, one would expect larger pegs with increased gravities, unless the rather remarkable situation exists that one gravity is the optimum or is greater than the optimum for peg-development. But how can one account for the more meager and very regular peg? This is undoubtedly due to all arch strains being overcome by the centrifuge, which removed this stimulus to the enlargement and unequal distribution of the peg.

It must not be forgotten that a centrifuge thus operated gives two mass accelerations at right angles to each other: one due to the centrifugal acceleration produced by the machine and acting in the direction of the pointing root, and one gravity downward. If a flat side of the seedling faces downward, and the machine gives a centrifugal acceleration of three gravities, three gravities act in the direction of the pointing root and one gravity downward. Such cultures showed very slight tendency to arch, and no greater peg-development on the lower than on the upper flank. If this organ were sensitive to gravity, one would expect it to show a greater response on the side where one extra gravity was acting, especially when the centrifugal acceleration was only three gravities. Of course it is entirely possible that WEBER'S law applies in such proportions that the application of one gravity as a stimulus cannot be perceived when three gravities are acting at right angles to it. In geotropism of *Vicia Faba* epicotyls, however, WEBER'S law applies in the proportion of 24–25, that is 4 per cent excess exposure to gravity in one direction is sufficient to give a response.

It must be remembered that while this experiment does not prove that gravity is not a direct stimulus in determining the size and lateral placement of the peg, it certainly furnishes no evidence that it is.

A detailed statement of the results of one experiment with Big Tom on a centrifuge with a horizontal axis will suffice to indicate the nature of the results obtained with that apparatus. Here, also, the coats were removed at the tip and the temperature kept at 23° C. by means of a spray. The revolutions were 440 per minute and the circles 3 and 6 inches in diameter. The 3-inch circle gives 8.25 gravities, while the 6-inch gives 16.5. In the 3-inch circle 15 were essentially pegless and 2 with slight two-sided pegs. In the 6-inch circle 25 were essentially pegless, 4 with slight two-sided pegs, and one with a peg toward one edge of the seed. The marked tendency to show pegless forms is manifested here, as in all experiments on the centrifuge, with three or more gravities. It seems that these accelerations prevent all disposition to arching and to arching nutations; hence they give many pegless forms.

OBLIQUE CLINOSTAT CULTURES

A number of cultures were made on the oblique clinostat as devised by FITTING.[10] The cultures were watered by a spray at 23° C. and grown with coats removed at the tip to avoid contact. The end of the clinostat axis to which the frame for bearing the seeds was attached was pointed upward from the horizontal, while the radicles of the seeds pointed toward the axis. This insures, as an understanding of the oblique clinostat will show, that extreme arching is avoided. The axis was placed at various angles with the horizontal, and the large plane of the seeds at corresponding angles with the axis. When the axis varied 5° from the horizontal, and the large plane of the seed was broken 5° from the axis, at one point in each revolution one flat face of the seed was exposed to gravity at an angle of 80° from the vertical (radicle pointing downward) and the other face at 90°. As soon as considerable growth occurs, of course geotropic response occurs in favor of the 90° exposure, and this throws the flank of 80° exposure more nearly

[10] See footnote 7.

90°, thereby avoiding sharp arching. The difference of exposure is marked then only in the early stages, and other exposures with 90° against 76° and 90° against 85° gave no peg-development in favor of the 90° either in the pumpkin or squash. It has been shown that the effectiveness of geotropic stimulus in orthotropic organs is approximately proportional to the sine of the angle, and therefore the 90° exposure is stronger than any of the others. If gravity is effective as a form stimulus in causing the lateral placement of the peg, we might expect it to be manifested by a larger peg-development on the flank exposed at 90°. These experiments give no indication of it, and yet it would hardly be expected that such differences in exposure would show an effect, since much greater differences failed to do so in the centrifuge experiments described above. It must also be pointed out that, unlike the centrifuge experiments, these experiments are rather unsatisfactory because the arching occurs in favor of the 90°, and that factor is sufficient, if great, to produce lateral placement of the peg. On this account, only angles differing rather slightly can be compared. It is evident, however, that these experiments, as do the centrifuge experiments, furnish no evidence that gravity is a direct stimulus to the lateral placement of the peg.

General and summary

As one sees from the experiments given above, there is *no evidence that gravity acts as a direct stimulus to the lateral placement of the peg.* Certainly, then, DARWIN is not justified in using this assumption as a main prop to a theory (mnemic theory) which itself looks away from rather than toward progress in the knowledge of plant response.

Assuming that all arching is avoided, the following facts seem to hold: the peg is to a considerable degree a natural integral part of the plant; it develops on all flanks of the hypocotyl approximately equal (granting perhaps that it is somewhat larger on the broad flanks in many of the cucurbits); it varies in size from the very slightest outgrowth appearing in a small percentage of Big Tom to the large pegs of the Hubbard squash.

It may be laid down with the formation of the seed, as in

Eucalyptus and *Cuphea*, where it is an equal ring all around the organ; or its formation may begin after germination, when its position and size are determined by the factors we have shown to be effective.

The lateral placement is apparently brought about by the arching of the hypocotyl. Two stimuli aid in the formation of the arch: contact of the coats and gravity. Contact of the coats is by far the more effective, for it will induce very sharp arching even against gravity.

In forms like the Boston marrow, gravity independent of contact with a deviation of 170° from the vertical gives strong enough arching to produce only 90 per cent with one-sided pegs. In Big Tom and various other forms it is somewhat more effective.

Arching leads to an increased development of the peg, as well as to its lateral placement, and in many cases it produces a peg where it would not otherwise appear, as in Big Tom. Contact likewise increases the size of the peg independent of its effect through arch-production.

No evidence obtained from this detailed study indicates that gravity, as a direct stimulus, in the least increases the peg-development.

THE UNIVERSITY OF CHICAGO

THE ORIGIN AND DEVELOPMENT OF BULBS IN THE GENUS ERYTHRONIUM[1]

FREDERICK H. BLODGETT

(WITH PLATES VIII–X AND SEVEN FIGURES)

Introduction

The genus *Erythronium* includes some fifteen species of bulbous plants of the north temperate zone, one of which occurs from the Pyrenees, across France, southern Europe, and Asia, to Korea and Japan. The remaining species are North American.

The plants are perennial through the annually renewed bulbs. These are developed at gradually increasing depths from the seedling to the flowering stage, after which they are formed at a nearly constant depth in the soil. The bulb consists of a few thick scales surrounding the stem apex; the aerial structures push upward from the base through the cavity inclosed by the inner scale. The first aerial structures are single leaves, two leaves and flowers appearing only after several years.

Special details of the development of one or another of the species have been examined by several writers; but some stages have been omitted in these accounts, and in others some obscurity exists as to the exact nature of the structures mentioned. A consecutive account of the development of the plant, with special reference to the origin and structure of the stem apex, and its outgrowths, from its inception in the embryo to the final formation of the flower bud, is the subject of this paper; which is thus a study of the vegetative development of the sporophyte, consideration of the gametophyte being omitted.

Erythronium americanum is taken as the basis of the study, since material of this species is abundant in the vicinity of Baltimore, and especially since it shows more specialization in its vegetative development than do the other forms. Comparisons have been made with other species, as will be noted, and the

[1] Contribution from the Botanical Laboratory of the Johns Hopkins University, no. 14.

differences found have a probable bearing upon the evolution of the genus.

Material was killed in chromacetic acid, and cut usually 10 μ in thickness; except in the case of the hard seeds, no special methods were necessary.

To Professor DUNCAN S. JOHNSON the author wishes to express his thanks for helpful criticism and maintained interest during the progress of the work.

Germination

The flowers of *Erythronium americanum* appear during the first week of April in this region, and the seeds ripen early in June, from which seedlings arise the following March. The main body of the seed measures about 4×2 mm., but a spongy spur at the chalaza and a fleshy raphe nearly double the bulk of the seed, subject to individual variation. The embryo in the ripe seed is slightly pointed toward the micropyle, but is otherwise undifferentiated (fig. 1).

Germination begins about the middle of September, when the seed becomes moistened by the fall rains, and the embryo begins to elongate. The growing embryo enlarges first to occupy the space filled by the spongy endosperm, in which it is imbedded, ordinarily by the first week of October. The tip of the cotyledon is organized into a haustorial organ, by which the hard endosperm is absorbed. Elongation proceeds slowly during the fall, so that the embryo is half the length of the seed in December (fig. 2). The rate of growth seems to be closely related to the abundance of moisture in the soil. The tip of the radicle is pushed about the end of the year through the micropyle. The stem apex at this stage appears in a narrow cavity extending from the surface nearly to the center of the tissue just behind the radicle. The hypocotyl does not elongate, and is practically absent. As the embryo continues to elongate, the stem apex is carried forward, and retains a constant position in relation to the radicle during the elongation of the cotyledon (fig. 3). The zone of elongation during this time is in the lower part of the cotyledon, just above the cavity in which the stem apex is situated. Growth is nearly vertical, and after penetrating the soil 1–3 cm. the descending axis comes to rest.

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When the endosperm has been exhausted, the elongation of the descending axis ceases. The zone of elongation in the cotyledon is now located near the upper end of the cotyledon, so that the tip of the cotyledon is withdrawn from the empty testa, and elevated into the light, much as in *Allium* (SACHS **18**). From the haustorial cells at the tip of the cotyledon two vascular bundles extend downward to the base of the root, just below the level of the stem apex, as in *Tulipa* (IRMISCH **11**). In some species (*E. grandiflorum*, and *E. Hartwegii*) there are three cotyledonary bundles (SARGANT **19**). After reaching the light, the cotyledon attains a total length of 8–10 cm. above the soil line (text fig. 6), and the elbow formed in the withdrawal from the seed coats gradually straightens. The cotyledon is cylindrical below, but may be considerably flattened in the upper portions, the two bundles lying side by side (figs. 4, 5).

The apical dome becomes differentiated during the descent of the stem apex, and the cavity in which it is inclosed changes into a curved pocket by the elongation of the walls of the cavity (figs. 6–10). The apex then rises as a dome from the bottom of the pocket. The space about the apex has a depth about equal to its width when the descending axis comes to rest. The thickness of the walls decreases from the axial to the opposite side, which lies immediately below the opening from the interior of the cavity to the exterior. The base of the cotyledon thus comes to form a sheath about the stem apex. The radicle has as yet grown but little; soon, however, the primary root is organized and advances from the end of the descending axis (text fig. 1). The primary root is the only one in the life cycle which responds positively to gravitation. At the base of the root a considerable cushion is formed, upon which root hairs are produced abundantly. By the growth of adjacent tissues the base of the root becomes oblique, and seems to be fused to the side of the cotyledonary sheath for a short distance (figs. 6–9). The stem apex, or plumule, has so far no vascular supply from the rest of the seedling, the cells below the apical dome being meristematic and undifferentiated as yet into tissues. The plumular trace is inserted upon each of the two cotyledonary bundles, just before they unite to form the root

stele, the region of fusion being about 0.5 mm. in length (figs. 16–20). This theoretically constitutes the "hypocotyl" in these seedlings (SARGANT 19).

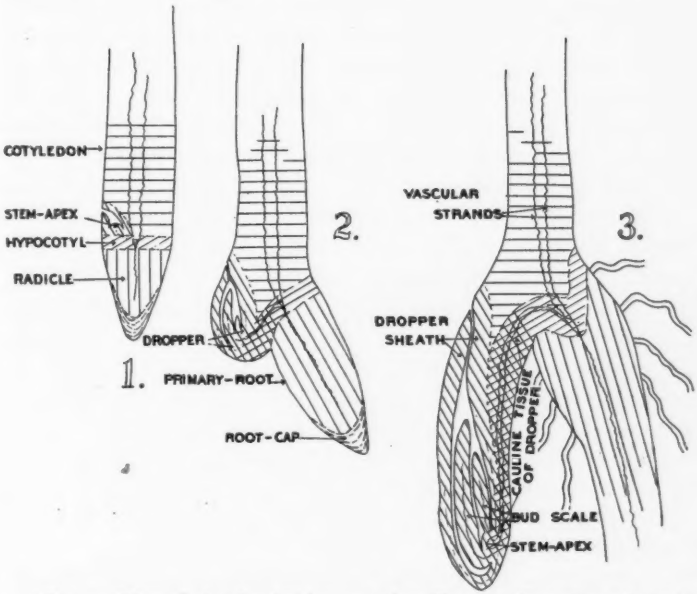

FIG. 1.—Diagram showing development of seedlings: *1*, descending axis during first stage; *2*, inception of droppers and development of root; *3*, dropper actively elongating downward, second stage of descent.

First vegetative period

The cotyledon functions as the first foliage leaf, and provides material for the further descent of the stem apex. Abundant stomata and large intercellular spaces are present in the body of the cotyledon; moreover it has the power of recovery from wilting to a high degree. This was found by allowing the soil to become dry and then watering, when seedlings which had become prostrate recovered their erect position, unless the cells had actually been killed. The cells nearest the tip were the first to show the effects of too great drying.

Soon after the cotyledon becomes active photosynthetically,

and the primary root is protruded into the soil from the end of the descending axis, the further descent of the stem apex begins. The sheath in the base of the cotyledon, in which the apical dome is located, elongates by the proliferation of the cells in the walls of the sheath so that the base of the cavity is lowered in reference to other points. As the structure so formed is positively geotropic in its growth response, it may conveniently be called a "dropper." The apical dome, being inserted at the base of the sheath, is carried forward in the elongation as a terminal bud (figs. 10, 13).

The dropper originates from the cotyledonary sheath through the irregular distribution of the dividing cells in the walls of the sheath. The base of the sheath is displaced laterally by the multiplication of cells between the apical dome and the axis of the cotyledon (figs. 6–8). This pushes the base outward from its original position. While the displacement is proceeding in the lateral direction, an elongation is also taking place, so that the dropper begins to push forward into the soil during its displacement. Soon after the axis of the dropper becomes established as a direction of growth, the zone of elongation becomes confined to the region immediately adjacent to the base of the apical dome. This places the growing tissue close to the apex of the dropper, as if it were a rhizome.

The inclosing walls of the dropper do not grow equally, the axial wall elongating more slowly at first than the abaxial, resulting in a lagging behind of the apical dome, in reference to the base of the sheath cavity. The stem apex thus becomes located on the side wall, instead of at the base of the sheath (fig. 13). The axis of the dome itself may become almost horizontal through this displacement. The oblique position of parts inaugurated at this stage of development persists through the life cycle, including the deep-seated bulbs of the flowering individuals. The lateral location of the stem apex at the base of the sheath cavity causes a distortion of the outgrowths from the apical dome as they appear. The apical outgrowths push upward into the cavity about the stem apex, and thereby appear to be at nearly right angles to the axis of the dome (fig. 13). The rate of growth of the apical dome and that of the developing scale is so nearly identical that the dome

itself is lost as a distinct group of cells. When the scale has so far developed that the margins of the leaf rudiment meet in front of the median line of the scale, then the apical dome becomes distinguishable again. The dome then forms a low mass of cells projecting from the face of the axial side of the scale into the space inclosed by the united margins. Continued growth soon makes the dome more conspicuous, and at the same time readjusts its position to a more central point (figs. 10, 12, 13). The tissues of the scale rudiment and of the stem apex are nearly alike in their staining qualities, and continue to be meristematic until a considerable size is reached. Thus in the first stages of scale formation, the growth in length of the apical dome and the growth in thickness of the scale rudiment are so nearly equal that there is no difference in staining reaction to aid in separating the two morphologically different tissues. It is not until the scale leaf has inclosed the apical dome by the forward growth of the margins of the scale, that the dome is to be separately recognized. This obscuring of the apical dome appears to be a recurring feature in the normal development of the bulbs, as the successive bulb scales are formed.

The dropper grows downward to a distance varying from a few millimeters to 4 (rarely 5) cm.; in most cases the dropper is about 2.5 cm. in length. This growth is accomplished during the period of activity of the cotyledon as a leaf, by which the needed starch and other materials are elaborated. At the end of three or four weeks of development, the apical bud within the dropper sheath becomes enlarged by the deposit of storage starch, and the stem apex with its inclosing bulb scale becomes the primary bulb (fig. 14). The seedling dies from the apex of the cotyledon backward, gradually involving all tissues except the bulb, which thus becomes isolated in the soil. The withered walls of the dropper sheath form a husk about the bulb. In the axil of the dropper sheath a bud is formed, which rarely develops.

During the active descent of the dropper, vascular connection from the stem apex to the base of the cotyledon is maintained through the bundles in the axial wall of the dropper. This tissue is to be regarded as cauline in character, since it terminates in the growing point of the stem. In its earliest stages the vascular

strand appears as a few elongated cells between the base of the apical dome and the base of the cotyledonary bundles (figs. 8–10, 16–20); as the dropper elongates these cells increase in number by additions at the growing end, and become more completely differentiated into vascular elements (figs. 8, 11, 13). At the end of the strand branches are given off into the scales developed from the apex. The vascular elements are only slightly developed in the bulb bundles, since there is little strength required, and the bundles are surrounded by abundant parenchyma. The spiral vessels are the most easily distinguished parts of the bundles.

During the summer the bulb shows no external signs of activity, but the stem apex is then organizing the first foliage leaf for the second vegetative season. In its inception the leaf resembles a scale leaf, but soon becomes differentiated into a blade and a basal portion. By the elongation of the base, the blade is elevated above the stem apex (fig. 15, *l*). The apical dome is thus left in a position simulating that of an axillary bud, with the leaf as its subtending organ. But the further development of the dome, as well as its immediately preceding history, identifies this as the stem apex. The leaf and the apical dome are in the relative development given about July 1.

In the development of the foliage leaf, the elongation of the petiole lifts the lamina above the stem apex before the latter becomes inclosed by the development of the margins of the blade. The margins grow outward from the median portion of the leaf rudiment, their edges passing each other above the level of the stem apex. The base of the petiole grows about the stem apex, so that this becomes inclosed in a sheath much as was the apical dome in the cotyledonary sheath. A small opening connects the cavity of the sheath with the space outside the petiole in the bulb.

At this time there appears in the axil of the leaf an axillary bud, which from its position in reference to the apical dome seems to be borne upon the surface of the dome, rather than to be truly axillary to the leaf. A bud is also developed in the axil of the inclosing scale. The stem apex develops usually two bulb scales during the late summer, thus forming a bulb rudiment at the base of the leaf by the close of the year. In these primary bulbs the stem

apex alone develops into a bulb in most cases; but in older plants the axillary buds may also develop into bulbs. When the bulbs of any age are renewed *in situ*, the apical bud forms the single new bulb; but when there are runners developed, the axillary buds also form bulbs, being then the terminal buds of runners which become isolated in the soil as in the case of the primary bulb from the dropper.

Second vegetative period

The second vegetative period in the life cycle of the individual begins in September, when the roots protrude from the base of the primary bulb. These are few in number, three in most cases, and do not respond positively to gravitation. The root rudiments originate just below the region where the vascular strands from the dropper give off branches into the stem apex and the bulb scales. These stages are shown at *r* in figs. 24, 26, 27. The roots grow nearly straight from the point of origin to their limit of growth. They maintain a spatial relation toward each other so as to be equidistant in the soil. The oblique position of the base of the bulb makes the cluster of roots which radiate from the base appear lateral (JOST **14**, p. 27) at the lower end of the bulb. In the older bulbs the roots are more numerous, and their lateral insertion is but slightly changed. The position of the roots in the soil is such as to define a nearly flat cone, with its axis in line with the axis of the apical dome. The angle taken by the axis of the cone varies slightly as the obliquity of the individual bulb differs, but lies close to 45° to the vertical. Under experimental tests, different positions of the bulbs used did not change the position of the axis of the cone of roots in reference to the axis of the apical dome, although the latter was itself placed in abnormal positions in respect to the vertical. Roots are rarely found within the conical mass of soil outlined by most of the roots; when so found, the roots are very numerous and some are crowded away from the peripheral portion of the meristem cells in the base of the bulb.

During their growth from the point of their inception to the surface of the bulb, the root rudiments pass through the tissues at the base of the bulb, a thickness of 1–3 mm. according to the size of the bulb. In passing through the bulb the advancing tip of

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The second vegetative period in the life cycle of the individual begins in September, when the roots protrude from the base of the primary bulb. These are few in number, three in most cases, and do not respond positively to gravitation. The root rudiments originate just below the region where the vascular strands from the dropper give off branches into the stem apex and the bulb scales. These stages are shown at *r* in figs. 24, 26, 27. The roots grow nearly straight from the point of origin to their limit of growth. They maintain a spatial relation toward each other so as to be equidistant in the soil. The oblique position of the base of the bulb makes the cluster of roots which radiate from the base appear lateral (Jost **14**, p. 27) at the lower end of the bulb. In the older bulbs the roots are more numerous, and their lateral insertion is but slightly changed. The position of the roots in the soil is such as to define a nearly flat cone, with its axis in line with the axis of the apical dome. The angle taken by the axis of the cone varies slightly as the obliquity of the individual bulb differs, but lies close to 45° to the vertical. Under experimental tests, different positions of the bulbs used did not change the position of the axis of the cone of roots in reference to the axis of the apical dome, although the latter was itself placed in abnormal positions in respect to the vertical. Roots are rarely found within the conical mass of soil outlined by most of the roots; when so found, the roots are very numerous and some are crowded away from the peripheral portion of the meristem cells in the base of the bulb.

During their growth from the point of their inception to the surface of the bulb, the root rudiments pass through the tissues at the base of the bulb, a thickness of 1–3 mm. according to the size of the bulb. In passing through the bulb the advancing tip of

the root rudiment appears to come into contact with the cell walls at intervals only. This is indicated in sections by the presence of a cavity about the root tip, the bulb parenchyma being separated from the root itself by a space in which there appear no cell walls. In the cells at a little distance from the line of advance of the root, scattered starch grains appear, and the normal starch content remains in the bulb parenchyma farther from the root cluster (text fig. 2). It appears that the starch is first removed from the cells in the path of the advancing root rudiments, then as the root is organized and grows forward, the cells themselves are disintegrated, leaving a clear pocket immediately about the conical end of the root. Only at the sides of these cavities were there any flattened cells, as if contact had occurred between the root tissue and the surrounding parenchyma. But as the root issues from the base into the soil, there is a collar of cells about the base, which constricts the root at this point to a slight degree.

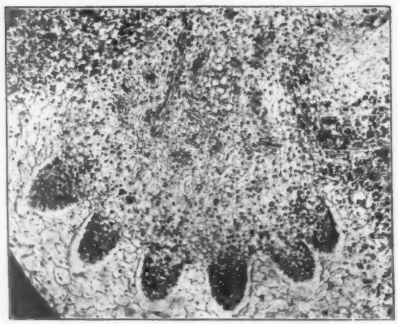

FIG. 2.—Base of bulb, showing inception of roots in summer; ×25.

The number of roots increases with the age of the bulb, in large flowering individuals reaching 30 or 40. These all die at the close of the season, and a new set is formed for the next year, even if the new bulb is developed *in situ*. The roots have no contractile cells, and act only as absorbing organs; the shape of the bulb helps to anchor the plant in place. Root hairs are produced in abundance in a moist chamber, or in nature on those parts of a root which may pass through an air space in the soil. Where the soil is in close contact with the root, the root hairs are inconspicuous or undeveloped (in this connection see **8**, p. 146). The meristem tissue from which the roots arise continues to form new root rudiments for some time after the main supply of roots is formed. Thus a new crop of roots may be formed after the already developed

one has been cut off; or if in handling the bulbs the roots present become dry, new roots are protruded among the bases of the old. In sections young rudiments are to be found in the basal tissue until nearly the close of the growing season.

The roots have a well-developed endodermis, formed of two, or rarely three, cell layers just outside the usually triarch stele (figs. 21, 22). The endodermis is delicate in the seedling, but well developed in the older roots.

The stem apex becomes more active after the roots are established in the soil, and develops the bulb rudiment from the apical bud. There are two axillary buds; one of these is in the axil of the first leaf (cotyledon), the base of which elongated to form the dropper, and on the death of the seedling dried out to form the husk. The other bud is axillary to the inner scale, which forms the bulk of the bulb as it lies in the soil until the second growing season begins. In the primary bulbs neither of these buds ordinarily develops further; but in older plants these, as well as the apical bud, form runners. During the mild periods of the winter and early spring the leaf is protruded from the bulb, and appears above the soil about the middle of March. The first leaves are about 1 cm. in width by 3–5 cm. in length, a little more tapering than the older leaves, but in other respects like them. They last for six to eight weeks, and then disappear by retrogressive withering. During their activity the bulb rudiment at the base of the petiole enlarges to its full size as the secondary bulb.

The starch stored in the primary bulb is used in part in the formation of the aerial structure (foliage leaf), in part also in the building of the new bulb. The bulb gradually disappears as the new bulb develops, the older tissues becoming free from starch and reacting to the Fehling test for sugar as the season advances and the new bulb enlarges. When the leaf begins to wither, in late May, there is practically nothing left of the primary bulb except its husk; this still incloses the base of the petiole, which forms the husk of the secondary bulb. After the death of the foliage leaf, the bulb is dormant until the roots are developed in September, as the first step in the third vegetative season. But in the interval the stem apex organizes the foliage leaf, and organizes the buds

in the axils of the two bulb scales as runner rudiments, in preparation for the next year. The details are similar to the same steps in the primary bulb.

Immature stages

Between the development of the secondary bulb and that of the bulb which bears a flowering shoot, an indefinite number of years may elapse. The least number of intervening seasons has been calculated to be three, making, with the first and second seasons, a minimum of five years from seed to seed. Many individuals at any stage fail to produce runners in any one season, and their immature period is correspondingly lengthened. Others fail to gain any depth in the development of the new bulbs from runners, and these also lengthen the interval between the first and final bulbs. With the production of the flower the activity of the primary stem apex ceases, the subsequent bulbs being developed annually each from a bud at the base of the aerial shoot. In the immature individuals more than one bulb is formed in average seasons in four species,[2] more or less specialized structures being developed for this purpose. Most of the plants producing runners in *E. americanum* in any one season after the second bulb have three at a time. One of these is the apical bud, the other two are axillary buds. The relation of these three buds is shown in figs. 28–33; these buds have been mentioned in a preceding paragraph as related to the development of the runners. The runners in the four species mentioned are not uniform in character, since in the development of the elongated structure of the runner different tissues are made use of by the plant in different species. *Erythronium americanum* is the most specialized in its development, but it is the clearest morphologically.

Each of the runners in *E. americanum* comes from a bud within the bulb (text fig. 3), the buds being made up finally of two scale leaves and a stem apex inclosed by them. The buds are inserted upon the tissues of the bulb in such a manner that the outer surface

[2] These are *E. americanum*, *E. albidum*, *E. propullans*, and *E. Hartwegii;* others rarely multiply. In *E. propullans* the adult plants have a lateral runner in addition to the renewal bulb within the old. Under cultivation axillary buds in adult bulbs in most species develop into bulbs.

of the external scale is united to the subtending portion of the bulb. As the buds begin their development, the first growth is eccentric and pushes the base of the bud outward from its first position, leaving the bottom of the bud free from contact with other tissues. Subsequent growth on the part of the bud is chiefly located in a zone about the base of the scale, close to the insertion of the inner scale upon the base of the bud. As the point at which the bud is united to the bulb tissue is above the zone of growth, the growing zone tends to push the base of the bud away from its original position and downward into the soil, as was the case in the beginning of the dropper. This elongation is confined almost entirely to the outer scale, the inner scale and the inclosed stem

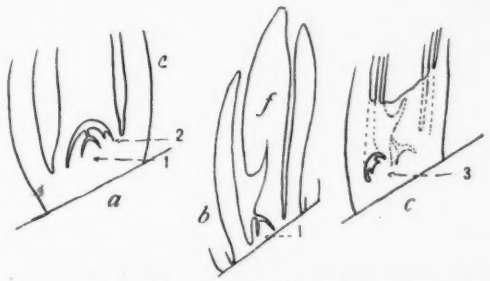

FIG. 3.—Space relations of buds in immature bulb of *E. americanum:* *1*, stem apex; *2*, inner axillary bud; *3*, outer axillary bud; ×10.

apex being carried along passively, as the terminal bud in the runner (cf. fig. 13). The runner is thus formed by the elongation of the outer scale of the bulb rudiment, and in the case of the apical bud and the inner axillary one, they burst through the inclosing base of the petiole when the base of the bulb has been penetrated. In these runners the scale is definitely organized in the bud, before any elongation begins, and the base of the foliage leaf takes no share in the formation of the runner, as did the base of the cotyledon in the seedling dropper. In other species[3] the sheathing base of the foliage leaf contributes to the developing runner, as in the case of the cotyledon and dropper. The elongation in this type of runner is the same as that in *Tulipa* (ROBERT-

[3] *E. albidum* for example.

SON 17, IRMISCH 10), in that the protrusion of the petiole base carries with it the bud inclosed by the petiole sheath.

In *E. albidum* two runners are usual, while the species from the western United States and Eurasia normally form but one. The length of the runner may be so much reduced as to pass unnoticed, but unusual conditions may demonstrate the presence of the typical structures not otherwise distinct. When but one runner is formed, or when the bulb is renewed *in situ*, the main stem apex is the active structure, the axillary buds if present remaining undeveloped.

There seems to be a moisture relation on the part of the growing runners. Plants of *E. americanum* growing in well-drained wood soil were found in several cases to have few runners; while other plants of similar general appearance, but in wet soil at the bottom of the same hill, showed runners in most individuals. It is noticeable about Baltimore that those individuals which grow in heavy, wet soils produce runners earlier and more abundantly than those of drier habitats. The development of abundant runners would hasten the attainment of full depth on the part of a particular group of plants, and this would be manifest in the greater frequency of flowering plants in a colony of stated size. The conditions under which the plants grow are evidently directly related to flower production, as the abundance of bloom has been observed to be associated with abundance of moisture in each of the habitats examined during the work here discussed.

In moist chamber experiments it was found that the tips of the runners were positively geotropic when lying on the top of saturated sphagnum, a little free water being present in the dish (fig. 23). In the absence of free water in the dish, the response was less marked, and in mere dampness it was a negligible quantity. In testing to determine whether the downward growth of the tips under abundant moisture is due to a moisture response or to gravitation, experiments were made with moist sphagnum in different positions in reference to the growing runners. The slow growth and the sluggish response on the part of the runners made the experiments inconclusive. In the moist chamber a period of two or three weeks was needed to carry through a set of tests.

The slow growth of the runners made experiments with them unsatisfactory when using the centrifuge or klinostat, but the evidence obtained tends to confirm the indifference to gravitation noted under natural conditions.

The lateral displacement of axillary buds, with little subsequent elongation, occurs in species of *Gagea* (IRMISCH 10). In *G. minima*, *G. lutea*, and *G. pratensis* there are short protrusions of the bulb rudiment as if about to form a runner, but the elongation is not sufficient to burst through the base of the bulb. The sheath in which the new bulb is formed is the base of one of the leaves, which forms a pouch or pocket about the enlarging bulb rudiment. In *Tulipa* the base of the petiole not only forms the pocket immediately about the bulb rudiment, but elongates in such a manner as to carry the inclosed bud forward into the soil as the terminal bud in a hollow runner. This is the type mentioned above as occurring in *Erythronium albidum* and others in respect to the apical bud. In each of these cases the bud tends to become deeper than its predecessor, but in *Allium vineale* and *A. Scorodophrasum* (IRMISCH 10) the buds are borne upon independent bases, which elongate during the growth of the buds, so that the the buds are elevated from the first position and thrust out of the top of the bulb. In the cases first mentioned the buds are attached laterally to the bulb tissue from which they arise, and are thus unable to rise above their insertion, but must descend more or less sharply in the individual species.

Structure of runners

The structure of the runner may be understood from the accompanying diagram (text fig. 4). Such a bud as that of *Allium vineale*, which elongates in the region below the insertion of the bud scales, would be elevated above its original position; this is the normal erect bud. On horizontal rhizomes a bud assumes the position shown in *2* of the diagram at the close of the period of elongation. If this position were taken during active progress through the soil, a great amount of resistance would have to be overcome in pushing the erect bud forward. This exact arrangement of parts has not been noticed in nature; but it occurs slightly modified in *Erythronium propullans*. In this species the

lateral runner issues from the side of the shoot with the bud at the tip in an erect position. But the bud does not stand freely exposed above the general surface of the runner stalk. The region immediately behind the bud, where the scale and cauline tissue are fused, thickens vertically, so that the bud receives the support of the adjacent tissue for its whole height, and is therefore not subject to transverse strain tending to invert it upon its base.

In the absence of supporting tissue for the height of the bud, the elongating runner would tend to advance the base of the bud

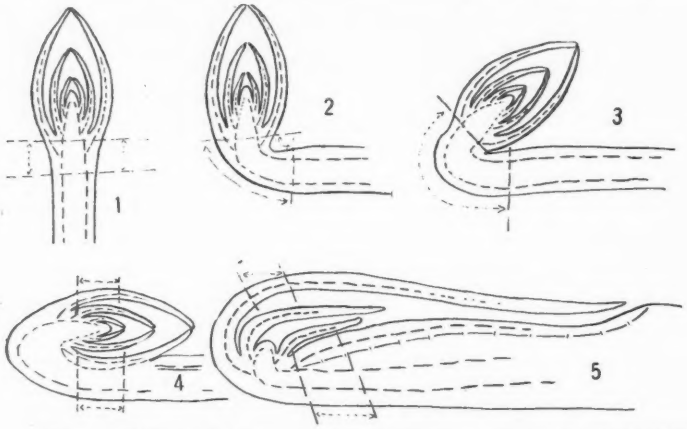

FIG. 4.—Evolution of *Erythronium* type of runner: *1*, normal bud, terminating stem (*Allium*); *2–4*, hypothetical stages, with horizontal stem; *5*, anatropous bud of *Erythronium* runners; dotted lines and arrows indicate zone of elongation in each case.

beyond the rest of the bud, as in no. *3*, since the unsupported parts of the bud would be retarded by friction in passing through the soil. The tendency under such conditions would be for the adjacent surfaces of the bud scale and the stalk to fuse, as suggested in no. *4*. Up to this point the scales of the bud have taken no part in the elongation of the runner or of the bud at the tip; but with the fusion of the bud with the surface of the runner stalk, either the zone of elongation must shift to a point outside the fusion region, or the scales must be included in the growing zone; otherwise the tissues would be under continued but irregular strains. In the

runners of *E. americanum* the structure sketched in no. 5 is present. The zone of elongation is close to the organic base of the bud, while the bud scale is fused for its full height with the stalk of the runner. There are no disruptive strains in this case, for the external scale of the bud elongates as fast as does the cauline tissue of the runner; that is, the scale leaf, like a foliage leaf of the same plant (ROBERTSON **17**), elongates in the basal zone; the stem elongates in its apical region, and as the two are folded back upon each other, the two growth regions are continuous about the inclosed bud. The position of this region of elongation is indicated by the space between the diagonal dotted lines in no. 5.

The cauline tissue in the runner is represented by the vascular bundles which unite the terminal bud in the runner tip to the base of the parent bulb. The presence of foliar tissue on the same side of the runner is indicated by the course of the vascular bundles, which turn backward at the base of the scale, and supply the inner face of the axial wall of the dropper in the same manner as the thin abaxial wall, where there is no tissue other than the scale. (Cf. text fig. 1.)

The runner habit

The plumule (stem apex) in the cotyledonary sheath does not form any bud scales which might by their elongation produce the dropper; but the walls of the cotyledonary sheath elongate after the primary root is established, and develop the dropper with the plumule as the terminal bud therein. This appears to be constant for all the species of the genus. In the subsequent stages in the several western species, and in *E. albidum* and *E. mesochoreum*, the main stem apex is thrust out as the runner bud within the elongated sheath formed by the clasping petiole. This is exactly comparable to the dropper of the seedling, in that the bud is carried forward passively and contributes nothing to the development of the structure. In the case of the second runner of *E. albidum* and of each of the three runners in *E. americanum*, the runner is formed by the bud itself forming the runner sheath by the elongation of its outer scale. The development of this type of runner introduces a new structure into the series present in the life cycle of the other species, and the degree to which this

lateral runner issues from the side of the shoot with the bud at the tip in an erect position. But the bud does not stand freely exposed above the general surface of the runner stalk. The region immediately behind the bud, where the scale and cauline tissue are fused, thickens vertically, so that the bud receives the support of the adjacent tissue for its whole height, and is therefore not subject to transverse strain tending to invert it upon its base.

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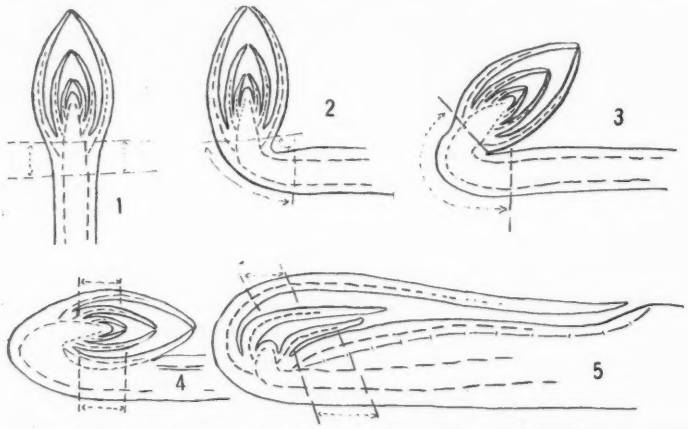

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innovation is developed may be taken as an index to the divergence from the original type. On this basis the most divergent species is *E. americanum*, with *E. albidum* and *E. mesochoreum* in order toward the type. *Erythronium propullans* is a special case, in which the bud axillary to the foliage leaf (text fig. 3, bud *2*) in immature plants (as of *E. americanum*) is functional in the mature individuals, being elevated above the base of the bulb by the growth at the base of the aerial shoot, as this raises the base of the leaves to their final position. In floral characters it is most nearly related to *E. albidum*. The reduced size of the flower is probably

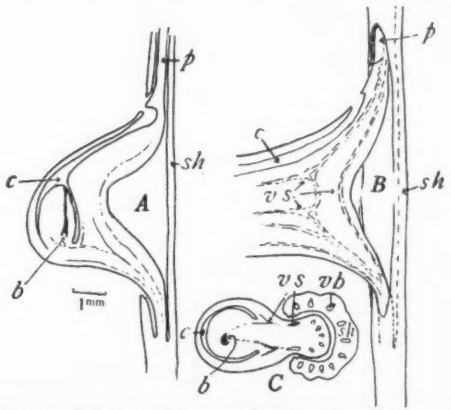

FIG. 5.—Offshoot of *E. propullans*, showing structure and vascular elements in sections: *A*, *C*, on base of older offshoot *B*; *b*, bud of offshoot; *c*, cavity about bud.

due in a measure to the interference with normal nutrition of the flower caused by the diversion of a portion of the vascular supply of the peduncle into the developing runner. The bud from which the lateral runner develops is inserted on the base of the peduncle in such a manner that in the early stages of growth as a runner the base of the peduncle elongates and thickens. As the clasping petioles (*sh*, text fig. 5) hold the upper part of the peduncle from freely moving upward, the result of elongation is to form an elbow, with the bud at the convex side of the bend. At this stage all the vascular bundles are diverted with the general distortion of the base of the peduncle (*A*). As the runner pushes forward from the

elbow of the peduncle, certain of the peduncle bundles produce branches which grow with the advance of the bud and maintain connection with the main vascular supply of the plant (*B*); but in so doing the total supply available to the peduncle is divided between the runner and the peduncle itself, and the reduced size of the flower appears to be the result.

In the species east of Colorado the aerial portions of the plant disintegrate with the ripening of the seeds, the fruit being prostrate when the seeds are ripe. The species of the Rocky Mountain region and westward do not become prostrate, but as the fruits ripen the stalk becomes a stiff and elastic wand, from the top of which the seeds are shaken. In these the capsule is revolute only at the apex, in the others the capsule splits completely to the base; among the first species the seeds are thrown out of the capsule by shaking; in the second group they are released by the rolling back of the inclosing walls of the prostrate capsule. The Eurasian species *E. Dens-canis* belongs to the second group in respect to its seed dispersal.

The western species differ from the forms of the eastern states in details of bulb development. In the eastern forms the region of fusion between the bulb tissues and those of the bud is small; and the sheath inclosing the bud, either in the case of the runner bulbs or when renewed *in situ*, is free from the developing bulb for most of its surface; but in the western forms the elongated bulb has a long fusion zone along the axial side, where the base of the sheath and the surface of the inclosed bud scale are fused. This appears as a ridge, from the edges of which the husk, in fully formed bulbs, extends around the rest of the bud. The bulbs are as a rule much more attenuate in the western forms than in the eastern, both in the young and in the adult stages. In immature bulbs the tip of the new bulb is often not at all lower than the base of the preceding bulb; this is due to the elongation upward on the part of the bud scales at a rate equal to that of the descent of the base of the new bulb in the petiole sheath. In the older bulbs the descent is decreased, but the elongation of the bulb scales upward from their bases produces the long bulbs characteristic of the group. In the bulbs examined, the species

from the western states have thinner husks than those of the eastern states, except *E. Hartwegii*, which has a tough and thick one like that of *Tulipa*. This form grows in an adobe soil, subject to high temperatures and considerable pressure when the soil dries, which may have its influence in the development of the heavier husk (WARMING 22). The Eurasian species (*E. Dens-canis*) has a very delicate husk, which becomes fragmentary during the development of the new bulb, so that the bulb is but slightly protected. The development of the bulb in this species is similar to that of the western forms, but the zone of fusion on the axial side of the bulb rudiment is more nearly the full height of the bulb scale than in these, extending almost to the tip of the scales, and the stem scar seems to be at the apex of the scale. As a result, the scales are fused together along their adaxial surfaces and the axillary buds are inserted much farther from the base of the bulb than is the case in any other species. The base of the petiole becomes charged with starch, and indistinguishable in appearance or function from a bulb scale. This explains the absence of a husk, formed in the other species from the drying of the sheathing petiolar sheath. The seedling of this species is similar to that of the rest of the genus, but there seems to be less of deepening growth in the immature stages than in any of the species of the United States. It is probable that the period of blooming is attained even more slowly by *E. Dens-canis* than in the other species, if the same relation of depth and flower production is maintained. In some of the western species grown in the Botanical Garden of Johns Hopkins University, it was noticed that they bloomed when the bulbs were much smaller in proportion to the average mature size than do those of the eastern forms. It may be that the same early blooming is present both in the Eurasian and in the western species, and that the bulbs continue to descend gradually during a long period after the blossoming habit is inaugurated. Such a point is physiological rather than morphological, and will not be discussed further at this time.

In the runners of *E. americanum* occasional "stimulation growths" have been noticed, apparently related to sudden excess of water. These are due to the bud inclosed by the runner bursting

through the tip of the runner, just as the runners burst the petiole sheath when first issuing from the bulb. The next scale of the bulb rudiment forms the runner extension, and the stem apex with a small scale is carried forward as if under normal conditions. The necessary nourishment for the added growth comes from the parent plant, through the stalk of the runner to the point where the terminal bud was inserted. Then the vascular bundles of the bud, following down through the bud scale, convey material to the stem apex in the tip of the extension of the runner. In two cases, in the spring of 1908, this extension of the runner by the protrusion of the terminal bud through the end of the runner sheath had been repeated a second time.

Development of the mature plants

The production of the flowers, which mark the maturity of the individual plant and the termination of the cycle of stages from seed to seed (text fig. 6), is associated with several changes from the manner of development followed during the immature condition. During the whole period from seedling to this stage, the primary stem apex has persisted, and from it have come the successive leaf rudiments which developed into either bulb scales or foliage leaves as the conditions demanded. The accompanying tabular view of the activity of the primary stem apex will show the general relation of these leaf rudiments. In addition to the outgrowths from the apical dome in the form of leaf rudiments, there have been various buds, axillary to the inner scale, which were laid down by the stem apex from time to time. The leaf rudiments developed in these axillary buds are not considered in the tabulated series of products from the stem apex. The bud in the axil of the outer scale does not arise from the apical tissue directly, but from the mass of meristem at the base of the scales.

The final structure developed from the primary stem apex, after passing through the immature stages, is the flower bud of the mature individual. In the immature stages the apical dome persists at the base of the bulb, producing successively the several bulb scales and foliage leaves. In the mature bulb the apical dome becomes surrounded by the foliage leaf rudiments (fig. 25),

and the whole structure becomes elevated above its original position by the elongation of the tissue below the insertion of the leaves. In the production of the flower bud, at the summit of the aerial shoot, the original stem apex comes to an end. The renewal bud for the next bulb is formed as a bud in the axil of the inner bulb scale, at the base of the shoot (figs. 25*b*, 26, 27).

GENERAL SEQUENCE OF FOLIAR OUTGROWTHS FROM THE STEM APEX IN ERYTHRONIUM AMERICANUM

Vegetative period	Foliar structures				Bulb sequences
	Sequence	Character	Function	Fate	
First	First leaf	Cotyledon	Photosynthesis	Withers	
	Second leaf	First scale	Dropper	Husk	
	Third leaf	Second scale	Storage	Bulb scale	Primary bulb
Second	Fourth leaf	First green leaf	Photosynthesis	Withers (husk?)	
	Fifth leaf	Third scale	Storage	Outer scale	
	Sixth leaf	Fourth scale	Storage	Inner scale	Second bulb
Third	Seventh leaf	Second green leaf	Photosynthesis	Withers*	
	Eighth leaf	Fifth scale	Runner	Husk	
	Ninth leaf	Sixth scale	Storage	Bulb scale	Third bulb
Fourth	Tenth leaf	Third green leaf	Photosynthesis	Withers*	
	Eleventh leaf	Seventh scale	Runner	Husk	
	Twelfth leaf	Eighth scale	Storage	Bulb scale	Fourth bulb
Fifth	Thirteenth leaf	Fourth green leaf	Photosynthesis	Withers*	
	Fourteenth leaf	Ninth scale	Storage	Outer scale	
	Fifteenth leaf	Tenth scale	Storage	Inner scale	Fifth bulb
	Sixteenth leaf	Fifth green leaf (and flower stalk)†	Photosynthesis	Withers	

* If the bulb is renewed *in situ*, the base of the leaf becomes the husk of the new bulb; if the new bulb develops as a runner bulb, the runner sheath forms the husk.

† With the development of the floral axis the activity of the primary stem apex ceases, a branch apex forming the renewal bulb thereafter.

This bud is evidently the homologue of bud *2*, of the immature stages, as indicated in text fig. 3. The bud is at first distinctly in the axil of the scale, but with the upward growth of the adjacent shoot it is lifted from its position to one on the base of the shoot itself (figs. 27 and 29, *3*).

The apical dome of this bud develops bulb scales during the

summer and develops into the full-sized bulb during the active period of the aerial shoot at the base of which it lies. Starch for storage is derived both from the photosynthesis of the leaves and from the deposits in the old bulb within which the new bulb

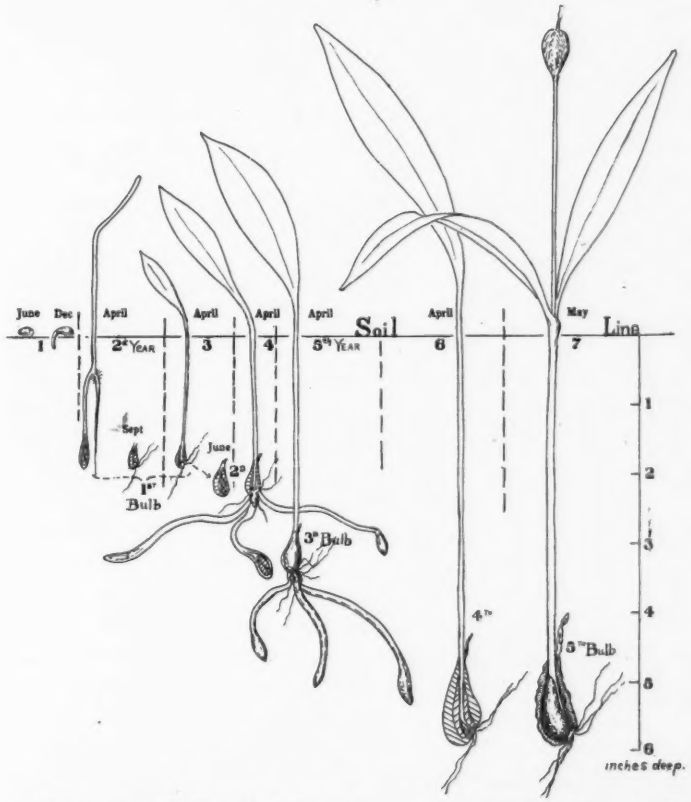

FIG. 6.—Stages in life cycle of *E. americanum:* under natural conditions the third bulb may repeat itself indefinitely, gaining little in depth, being renewed *in situ* for one or more seasons.

is formed. By the time the aerial shoot is dead, the new bulb is mature, and the apical dome within it lays down the rudiments of the next flower. This process is repeated indefinitely, the

individual becoming more robust with time, but otherwise remaining the same. A very slight increase in depth occurs as time passes, since the new bulbs are a little larger than their predecessors, and the new bulb is formed below the center of the old one which it replaces. But a bulb once flowering may revert to the sterile condition after a series of years. Bulbs which have been dug from the soil and allowed to become somewhat dried out are apt to "break," that is, to produce two or three small bulbs instead of the single large one customary in the flowering plants. Bulbs so produced are sterile for at least two years, as found by experiment. This is especially apt to occur if the bulbs are dug while the shoot is actively growing upward through the soil in the spring. Removal of the soil close to a bulb of a flowering plant often causes such to revert to the immature condition and produce runners, even though the flowering of the current season is not hindered by the changed soil conditions.

Individual plants of any age may force the bulb rudiments into abnormal development under the stimulation of unfavorable conditions. A large number of bulbs of various sizes were dug soon after the leaves had pushed through the soil. These with a little soil were left in a tin box for several days; the box was well wrapped and left in a cool room in the meanwhile. Upon inspection ten days later, the leaves were found to have shriveled away, but the bulbs had formed a small bulb from each of the buds which under normal conditions would have developed runners. The starch present in the old bulb and in the leaf furnished the material for the new bulbs, aside from water, which was in the moist soil. This was repeated several times, the exact details varying with the exact condition of the bulbs when dug from the soil. Thus if the runner is already pushing through the base of the bulb, or is further developed, it continues to elongate for several days, but in the end will form the terminal bud into the bulb; it apparently transfers to it the substance of the old bulb and runner stalk as if under normal conditions.

In the descriptions of the liliaceous ovary, the placentae are usually said to come from the incurved margins of the carpellary leaves. In *Erythronium*, however, the margins of the carpels

appear to come into blunt contact, but do not curve inward. The margins unite along the line of contact, and the partitions are formed from a median rib projecting inward from each carpel (figs. 34, 35), meeting at the center of the ovary (TEMPLE 21). In the full-grown ovary, as at fertilization, the evidence for this interpretation of the case is found in the double bundles along the line of dehiscence in the walls of the ovary, and in the presence of a layer of cells rich in protoplasm which passes around the end of the abutting partitions as they come into contact at the center of the ovary (text fig. 7). The densely protoplasmic cells which line the ovary along the line of the placentae continue around the end of each median wing, as shown in the photograph. This series of surfaces of slight contact determines the dehiscence of the ripe capsule.

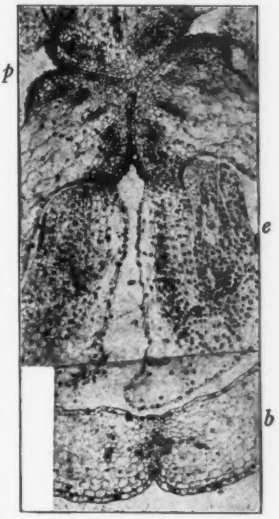

FIG. 7.—Transverse section of fertilized ovary of *E. americanum*, showing abutting placentae (*p*), two-celled embryo (*e*), and double bundle at edges of fused carpels (*b*); ×25.

Occasional plants are found with sterile anthers on one or more of the stamens, some patches showing many of the plants with no functional pollen. It has been found that the sterility of the anthers begins at least as early as the divisions of the pollen mother cells, as buds have been examined in which three of the anthers were normal, and had normal pollen grains; while the sporogenous tissue of the others was degenerating (fig. 35, *m*, *m'*); the other tissues of the anthers were normal in appearance. In the field it has been noticed that the plants with dark pollen on the stigma had the larger fruits and the larger number of seeds. Plants having pale anthers often lacked pollen entirely, and their seed-developing power seemed to be deficient also. The plants of the two types, fertile with dark stamens and poor with pale anthers, each occur in patches often of considerable numbers. This may

account for the poor set of seed in such cases, for insects working over the patch would not bring in so much viable pollen to the weak plants as if there was a commingling of the two.

Development of seeds

The fertilized ovule enlarges rapidly, mainly through the growth of the embryo sac. The sac destroys the nucellus except a crushed remnant at the bottom of the sac. The raphe and chalazal spur enlarge at the same time, and add to the bulk of the seed as a whole. The endosperm develops slowly, remaining for a considerable time as a layer lining the wall of the sac between the base and the suspensor at the tip. The embryo first develops a considerable mass of cells in the micropylar end of the sac, from the inner free surface of which the functional embryogenic cells are developed (COULTER **7**). This inner surface may become lobed, and then gives the condition called polyembryony by JEFFREY (**13**) and SCHAFFNER (**20**). Twin embryos developed in one case out of several hundred seeds germinated in this work; these were united near the upper end, but completely free below, and their vascular systems were distinct. These embryos probably were formed from two adjacent lobes from the free surface of the suspensor, becoming united through the incorporation of some cells in common from the base of the lobes. In pushing into the soil, the elongation had occurred in the zone just behind the stem apex, and this was distinct in each of the two embryos, producing the condition shown (fig. 36).

The general conditions of the sac, endosperm, and suspensor in *E. americanum* are closely duplicated in *Urtica cannabina*, as studied by MODILEWSKY (**15**). In both cases there is a thin lining of free endosperm nuclei along the walls of the sac, a considerable suspensor at the tip, and a mass of deeply staining cells below the base of the sac. In *Erythronium* these cells form a considerable mass, and extend backward to the termination of the raphal bundle at the chalaza. These cells stain deeply even in ripe seeds, and the adjacent cells of the remnant of the nucellus remain in close contact with the center of the base of the endosperm in the ripe seed. This would indicate the purpose of these cells

to be that of transfer agents for substances from the chalaza to the embryo sac, and thence to the forming embryo and endosperm.

When the seed reaches its full development the embryo sac is filled with hard endosperm of reserve cellulose. The cells in the endosperm have their longer axes directed inward from the periphery, curving somewhat toward the micropylar end of the seed. Through the center of the endosperm there is sometimes the same cellular endosperm as elsewhere, more frequently this is nearly solid cellulose. Immediately about the embryo there is usually a small mass of less firm endosperm, which in some cases extends to the surface of the seed, filling the space earlier occupied by the suspensor. It is probable that germination is aided materially in such cases, as moisture can more promptly reach the embryo by this path than would be the case if only thick-walled endosperm were present. At the base of the seed the endosperm shows considerable shrinking, with the remnant of the nucellus remaining in contact with the endosperm for a small area near the center. This secures contact between the hard endosperm and the spongy spur, and even when the spur has disappeared the inner layers of the tissue at the chalaza remain in intimate contact with the base of the endosperm. As the endosperm along the axis of the embryo sac is the last to be deposited, it is probable that the mass of spongy cells in contact with the base is of advantage in the imbibition of water preliminary to germination. In different seeds the exact appearance of the central portion of the endosperm varies from nearly solid, with infrequent cell cavities, to a condition similar to that of the peripheral endosperm; the latter is less common than is the solid core mass. The exact distribution of the cell cavities in the endosperm is probably in close relation to the moisture conditions during the late stages of ripening of the seed. In germination the embryo first enlarges to occupy the space filled by the spongy endosperm in which it lies; then the cotyledon, acting as a haustorial organ, dissolves a path for itself along the axis of the endosperm. The solvent action extends along the lines of cell cavities toward the periphery, and the endosperm is absorbed almost completely.

Completion of the cycle

The individual which began with the germination of the seed and the organization of the stem apex in the sheath at the base of the cotyledon, has been followed through the series of changes normal to its development as *Erythronium americanum*, and the variations have been indicated between this species and the others of the genus. The cycle of the sporophytic generation is thus completed, and the original stem apex culminates in the formation of the flower parts of the first blossom produced by the bulb on reaching maturity. It was shown that the species were structurally related with a large group, the western species, behaving similarly, the others diverging more or less from the habits of these forms. The structures involved in the divergence from type are those most active in the immature stages, and most freely produced in *E. americanum*. This species, therefore, has been regarded here as the most remote from the ancestral form, since the majority of the species are of the more simple type of development in the vegetative habits. The species having the uniform vegetative habits are native to the region from the Rocky Mountains westward, becoming more abundant in species as the Pacific coast is approached, and culminating in a series of habitats in southwestern Oregon. This may be assumed to be near the original home of the genus, from which the distribution and differentiation into the present habitats and species have occurred. It is probable that the lines of migration have followed the present lines of specific distribution, especially in the United States. The single species of Eurasia combines the bulb characters of the western species with the withering aerial parts of the eastern forms. The character of the habitats in which this species occurs may be so nearly uniform that no marked variations have been developed from the original type, beyond that involved in the prostrate fruit. Ants have been observed carrying the seeds of *E. americanum*, and it is probable that they aid in distribution in each of the species having seeds with fleshy raphe or spur tissue. This would include *E. Denscanis* as one of the myrmechochorous species, as a considerable chalazal spur is present, comparable to that of *Viola* or *Sanguinaria* (BEAL 1), but not so large as that of *E. americanum* or *E. albidum*.

Summary

The points presented in this paper may be summarized as follows:

The undifferentiated embryo begins to elongate in the fall and organizes a rudimentary stem apex in a narrow cavity at the base of the cotyledon. In germination the radicle is thrust into the soil during the winter, the stem apex following immediately behind the base of the radicle, in the cavity mentioned. The hypocotyl is represented by the fusion region between the vascular supply to the stem apex and the main vascular system of the seedling; it takes no part in the development of the seedling. After absorbing the endosperm, the cotyledon is elevated into the air, and acts as the first photosynthetic organ. Either two or three vascular bundles are present, varying with the species.

During the activity of the cotyledon as a leaf, the cavity in the base of the cotyledon about the stem apex elongates to form a slender sheath, with the stem apex inclosed as a terminal bud at the tip. The "dropper" so formed is positively geotropic in response, as is the primary root; the runners and roots of later stages are not positively geotropic. At the close of the season the terminal bud of the dropper is isolated in the soil by the withering of other parts of the plant.

During the summer the first foliage leaf is organized by the stem apex and becomes functional the following spring. Roots are protruded at the base of the bulb in the fall, which marks the beginning of the second vegetative period. This sequence of development is repeated in the subsequent seasons to the mature bulbs.

The stem apex becomes inclosed by the base of the foliage leaf, and there forms a bud from which the next bulb will develop. When the bulb is renewed *in situ*, only this bud develops; this is also the rule in the species producing but one runner. In *E. americanum* two buds are usually formed in addition to the main bud, each of which elongates as a runner and forms a bulb. These additional runners spring from buds axillary to the leaf, or to a bulb scale. When but one runner is developed normally by a species, it is formed from the elongation of the base of the petiole, which carries the bulb rudiment into the soil as a terminal bud,

as in *Tulipa*. The additional runners when present, and all three in *E. americanum*, are developed from the elongation of the outer scale of the bud, the inner scale and the apical dome forming the terminal bud of such a runner.

The vascular connection between the stem apex and the point of insertion of the runner is to be considered cauline, the rest of the runner tissue as foliar and apical. The structure of the runner in *E. americanum* is that of an anatropous bud, the outer surface of its external scale being fused with the upper surface of the supporting stem; the latter maintains vascular connection between the base and the apex of the structure developed. The zone of growth of the fusion structure is located as in normal rhizomes, close to the tip of the structure; both the scale and the cauline tissue take part in the elongation.

The mature plants form the floral shoot from the stem apex, the new bulb being developed from a bud, at the base of the shoot. The stem apex of the new bud forms the next flower, and the bulb is renewed in turn from a bud axillary to the inner scale of the bulb rudiment. The bud in the axil of the outer scale usually dies without developing.

Using the runner habit as the basis of comparison, the genus is divided into two groups, one occurring typically at low elevation, and producing two or three slender runners from short bulbs, the other at higher elevation and forming but one runner and developing into slender bulbs. A form intermediate between the two occurs in western Kansas and Nebraska. An aberrant form occurs in a restricted locality in Minnesota, having a lateral runner developed from a bud in the axil of a foliage leaf.

The interval between germination and flowering on the part of an individual is at least six years. This minimum is liable to indefinite increase under average conditions, by the interpolation of additional immature bulbs because of the formation of the runner bulbs no deeper than the parent bulb, or by the suppression of runners in a particular year.

The distribution of the species points to the Pacific coast as the probable home of the genus, the present distribution being the result of migration along lines connecting the habitats of the

present forms. The species are found to vary from the type found in the assumed original habitat approximately in proportion to the distance of migration. The species of Eurasia combines features of the two groups in its vegetative characters.

The roots radiate from a point near the base of the bulb, but show no definite response to gravity; they maintain a definite space relation to each other, defining the surface of a cone in the soil, the axis of which is about 45° to the vertical. In development, the roots arise in September from cells just below the vascular base of the bulb, and grow in straight lines during their elongation. In penetrating the bulb tissue, the cells are apparently dissolved by the root tissue, making a cavity about the advancing root rudiments. The number of roots increases with the age of the bulb.

Conclusions

From the foregoing study the following conclusions may be drawn: The delayed development of the embryo is associated with a large store of endosperm; this is drawn upon by the germinating embryo during the season when vegetative activity is low; the young seedling is established in the soil early in the spring, the endosperm furnishing the needed materials for its development. With the exhaustion of the reserve material of the seed, the primary root is developed, and the cotyledon is elevated into the air and light; the cotyledon is the only leaf exposed to the light by the seedling. The stem apex, located in a narrow cavity in the base of the cotyledon, is carried forward by the elongation of the embryo, and, after the elevation of the cotyledon, is carried farther into the soil by the elongation of the walls of the cavity. The short period of vegetative activity, and the prompt descent of the stem apex in the dropper, would indicate adjustment to short growing seasons; the brevity of the active season is a feature of the life cycle. The tendency on the part of the seedling to bury the stem apex deeply is continued by the immature plants in the production of runners; in some cases these are strictly comparable to the dropper of the seedling in structure, in others they involve new developments; but the result is the same in either case.

The persistence of the original stem apex until the establish-

ment of the flower axis allows for the repetition of an indefinite series of immature bulbs, formed from runners or *in situ*, but introducing no new structures during the whole period of immature development. With the formation of the flowering shoot, the vegetative structures become secondary in importance, and the renewal bulb is developed from an axillary bud at the base of the shoot. The continuation of the individual is thereafter without vegetative multiplication normally, the increase being secured by the seeds.

The geographical distribution of species and their relation to each other in structural details indicate that the genus originated in that region of the Pacific coast now included in the state of Oregon, and has been distributed along lines approximately following the present habitats of the several species. In the progress of migration the advancing species developed special methods for rapid descent into the soil, which in some forms has become a means of numerical increase.

In the development of means of vegetative multiplication, elongation of the structure immediately about the stem apex (in the seedling the base of the cotyledon, in the western forms the base of the petiole) was followed by the elongation of the scales of axillary buds, thus forming additional descending axes, each of which developed an additional bulb from its terminal bud. One species has developed a runner from a bud axillary to the foliage leaf, apparently being derived from the adjacent form in which the second runner arises from a bud axillary to the inner scale. The production of this lateral runner is confined to the flowering plants, since only in these is the leaf axil elevated above the base of the bulb. This form is very restricted, and appears to be the species most recently derived from the parent stock, or from some other species as these are now known.

The general development in the genus would confirm the assumption that it is related to *Tulipa*, especially through *T. sylvestris*.

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EXPLANATION OF PLATES VIII–X

PLATE VIII

All figures drawn on the same scale, which is indicated by the measured line; drawings made by means of a vertical projecting lantern from the stained sections.

FIG. 1.—Dormant embryo in endosperm; *i*, remnant of inner integument.

FIG. 2.—Embryo about December 1, still within seed; *s*, position of stem apex; *e*, endosperm.

FIG. 3.—Descending tip of seedling; stem apex in slit at *a*.

FIG. 3*a*.—Cross-section of seedling at line *a–b* of fig. 3.

FIG. 4.—Tip of cotyledon in longitudinal section, showing haustorial cells (*h*) and vascular cells (*v*).

FIG. 5.—Cross-section of cotyledon; *v*, vascular bundles; *s*, stomata.

FIGS. 6–13.—Stages in the development of the dropper about the stem apex (*s*).

FIGS. 11, 12.—Two sections of the same dropper, showing scale leaf (*l*) and stem apex (*s*); *t*, plumule trace.

FIG. 13.—Stem apex as terminal bud in tip of active dropper, as in April.

PLATE IX

Magnification the same as in plate VIII, except in figs. 21, 22, 23, 25, in which the magnification is indicated.

FIG. 14.—Stem apex in late June at bottom of bulb.

FIG. 15.—Stem apex (*s*) and rudiment of foliage leaf (*l*) in July.

FIGS. 16–20.—Cross-sections of young dropper, from base of cotyledon downward, showing hypocotyl region (17), separation of root and dropper (18), and dome of stem apex (20).

FIGS. 21, 22.—Cross-sections of active and dead root steles; *e*, endodermis; ×250.

FIG. 23.—Active runner marked to show zone of maximum elongation after three weeks' growth; natural size.

FIG. 24.—Base of bulb, showing sheathing petiole (*p*), stem apex (*s*), and root rudiment (*r*), as found August 1.

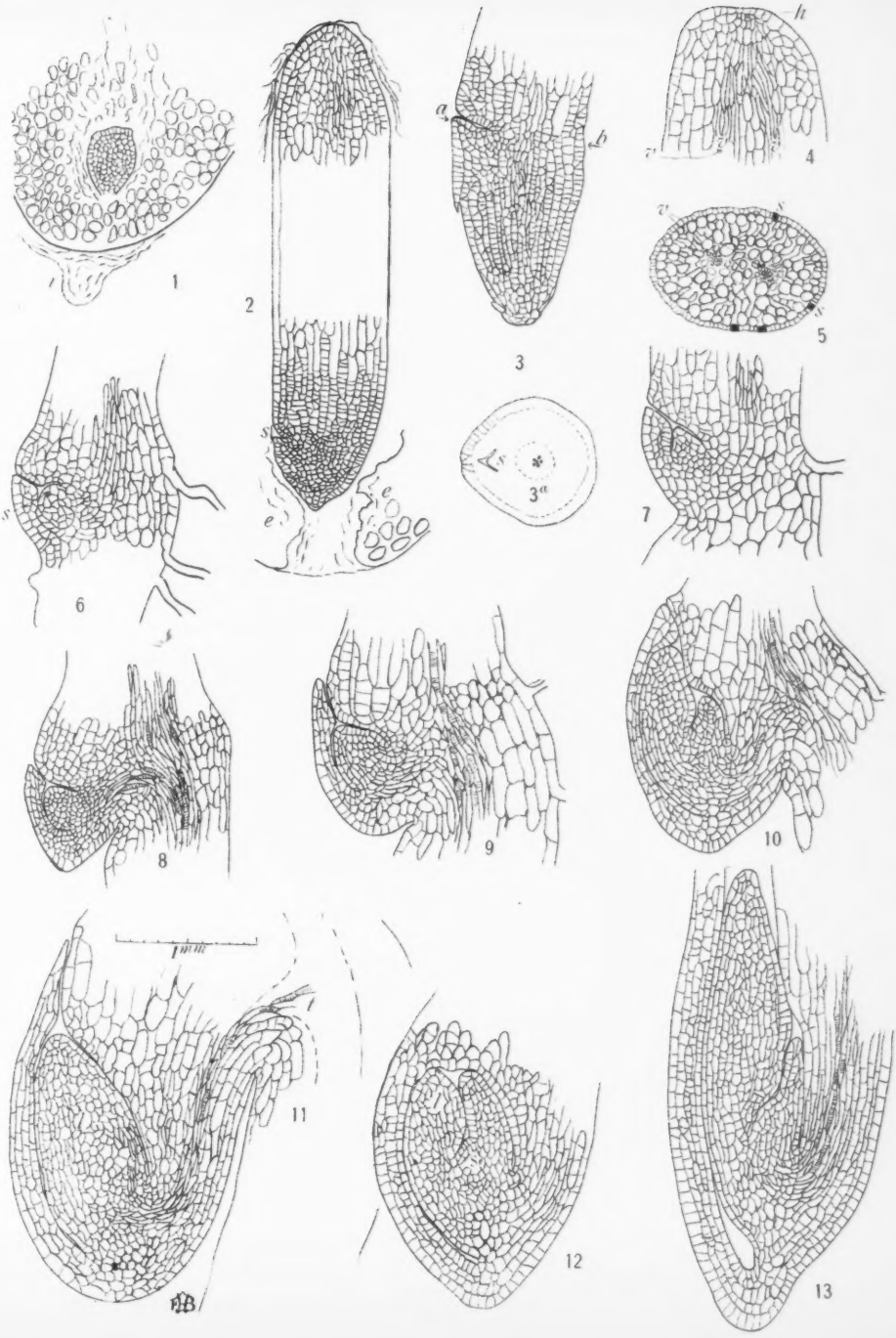
FIG. 25.—Outline of stem apex in flowering bulb, showing flower rudiment (*f*) inclosed by the foliage leaves (*l*) and the location of the renewal bud (*b*); ×10.

FIG. 26.—Renewal bud from the same section showing apical dome above and root rudiment below the scale; July 1.

FIG. 27.—The same structures about August 1, on the same scale.

PLATE X

Figs. 28, 28*a*, 34, 35 on a uniform scale, the same as in previous figures; figs. 29–33, 36 as indicated.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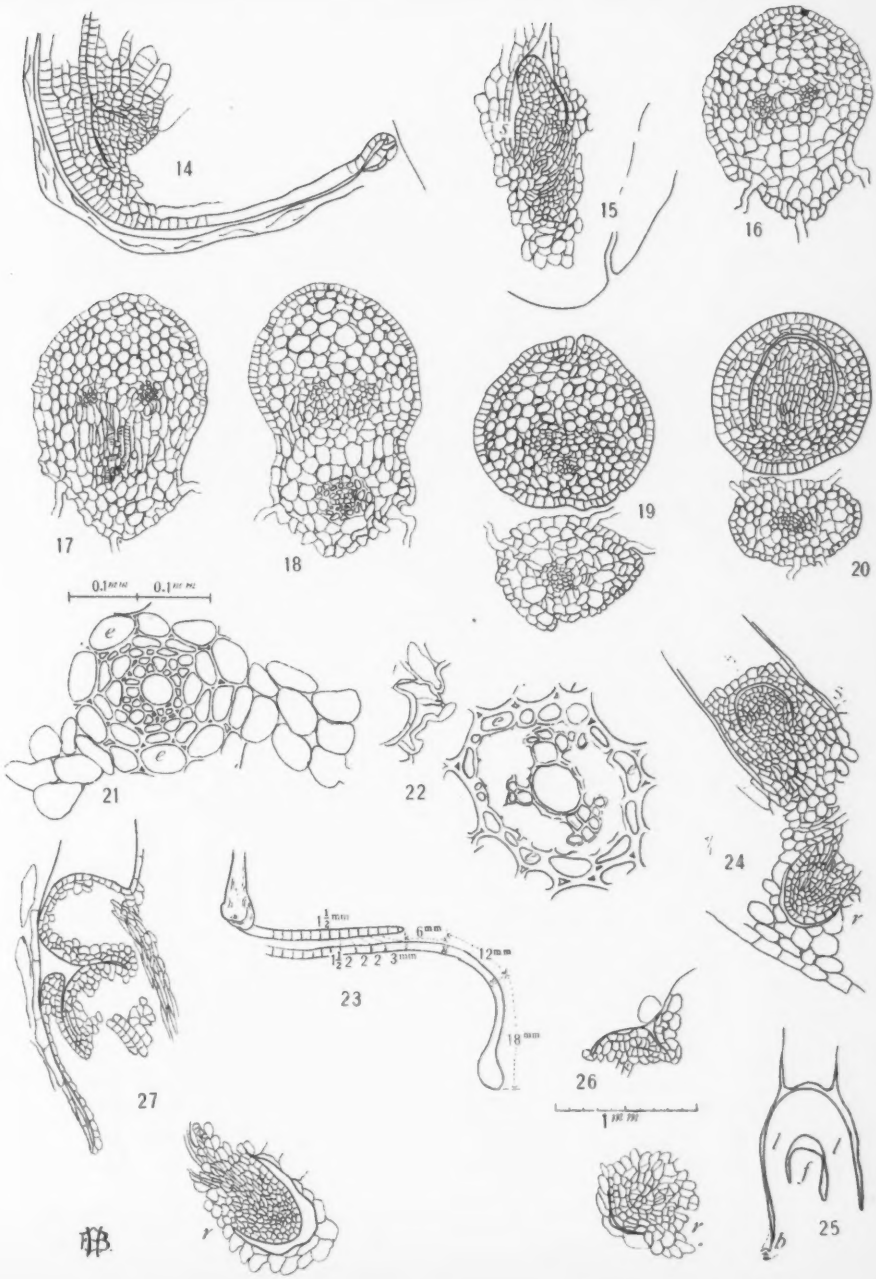
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28
28a
29
30
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33
34
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1 mm

FIG. 28.—The three buds in the immature bulbs of *E. americanum;* main stem apex; *2*, bud axillary to leaf; *3*, bud axillary to scale; *1* and *3* on the same section.

FIG. 28*a*.—Sagittal section of bud *3*, to show apical dome.

FIG. 29.—Outline of entire section shown in fig. 28; relation of buds *1* and *3*.

FIG. 30.—Similar section in reference to bud *2;* in each the sheathing base of the petiole is *p*.

FIGS. 31–33.—Cross-sections of bulb rudiment, showing relation of the same structures as shown in figs. 28–30; the sections follow in order of their numbers but are not consecutive.

FIGS. 34, 35.—Cross-sections of developing flower bud in early September and early December, on the same scale and in the same orientation; *f*, foliage leaves; *p*, petals; *s*, stamens; *o*, ovary wall; *l*, line of dehiscence (lateral margin of carpel); *w*, wing-placenta from median region of carpel; *m*, *m'*, normal and degenerating microspores.

FIG. 36.—Twin embryos of *E. americanum*, ×5; the union of the two cotyledons shown below in outline.

REVERSIONARY CHARACTERS OF TRAUMATIC OAK WOODS[1]

IRVING W. BAILEY

(WITH PLATES XI AND XII)

In studying the phylogeny of plants there are certain principles or canons of comparative anatomy which have been formulated within recent years by morphologists and anatomists. Thus the application, to seedling plants, of HAECKEL's law of recapitulation for stages in ontogenesis has been strikingly illustrated by STRASBURGER, GOEBEL, JEFFREY, EAMES, and others. Furthermore, the persistency of ancestral characters in certain regions of plants has been well established. In this connection the researches of SOLMS-LAUBACH, SCOTT, and JEFFREY have shown conclusively that the cone axis is often the seat of primitive characters. The importance of foliar organs in connection with ancestral characters has been shown by SCOTT, JEFFREY, and FAULL. JEFFREY has further pointed out in his memoir on *Sequoia*[2] the importance of vigorous cone-bearing branches of *Sequoia gigantea* as the seat of recapitulation of ancestral conditions. The importance of hypertrophied or wounded areas as the seat of reversion to primitive characters is strongly appreciated by zoologists. This principle has also been applied to the traumatic areas of plants by JEFFREY, who has pointed out the traumatic reversionary origin of resin canals in the wood of the higher Abietineae,[3] certain Sequoiineae,[4] and the older Araucarineae,[5] which normally possess none of these

[1] Contributions from the Phanerogamic Laboratories of Harvard University, no. 24.

[2] The comparative anatomy and phylogeny of the Coniferales. I. The genus *Sequoia*. Mem. Boston Soc. Nat. Hist. **5**:441–459. *pls. 68–71*. 1903.

[3] The comparative anatomy and phylogeny of the Coniferales. II. The Abietineae. Mem. Boston Soc. Nat. Hist. **6**:1–37. *pls. 1–7*. 1904.

[4] The comparative anatomy and phylogeny of the Coniferales. I. The genus *Sequoia*. Mem. Boston Soc. Nat. Hist. **5**:441–459. *pls. 68–71*. 1903.

[5] The wound reactions of *Brachyphyllum*. Annals of Botany **20**:383–394. *pls. 27, 28*. 1906.

Araucariopitys, a new genus of araucarians. BOT. GAZETTE **44**:435–444. *pls. 28–30*. 1907.

structures; and has demonstrated the presence of traumatic marginal tracheids in the wounded wood of *Cunninghamia sinensis*.[6]

An interesting parallel to the work of JEFFREY upon traumatic reversions in the Coniferales has been noted by the writer in the traumatic reversions of wounded oak wood. Owing to the controversy which exists as to the relative primitiveness of the Abietineae and Cupressineae this occurrence of traumatic reversions in a dicotyledonous genus is of particular interest in demonstrating the application of the principles of experimental morphology to plants.

Before describing the reversionary characters of oaks, it will be well to have clearly in mind the normal structure of the wood of existing oaks, and also that of ancestral types. As is well known, the secondary xylem of living oaks consists of vessels, fibers, tracheids, and parenchyma. The last occurs vertically as wood parenchyma, and horizontally disposed in plates of tissue extending radially, the so-called primary and secondary medullary rays. The "primary rays" (fig. 1) are the distinctive feature of oak wood, the "silver grain," and are broad, fusiform masses, many cells in width, which are supposed to originate as inclusions of fundamental tissue between the primary fibrovascular bundles. The "secondary rays" are thin sheets of tissue, and consist of a single row of cells when seen in tangential or transverse section (fig. 1). These rays, unlike the primary rays, are supposed to originate only with secondary growth.

In contrast to this type of structure occurring in the mature wood of extant oaks, EAMES has shown[7] that certain miocene oaks do not possess large rays composed of homogeneous masses of ray parenchyma, but have in their place bands of aggregated smaller rays which are separated by fibers and wood parenchyma. These rays are homologous with the "false rays" of the Betulaceae, and lead to the conclusion that the so-called primary rays of extant oaks have been built up by an aggregation and fusion of numerous originally uniseriate rays.

[6] Traumatic ray tracheids in *Cunninghamia sinensis*. Annals of Botany **22**:593–602. *pl. 31*. 1908.

[7] On the origin of the broad ray in *Quercus*. BOT. GAZETTE **49**:161–166. *pls. 8, 9*. 1910.

The writer has shown,[8] by a study of numerous species of Betulaceae and Fagaceae, that ample evidence of a compounding process exists in the rays of many living oaks, alders, birches, and hornbeams. Thus many American live oaks (fig. 5) possess bands of aggregated rays which are similar to the false rays of the Betulaceae. Among alders and birches species may be found with non-aggregated uniseriate rays, aggregated small rays, and large homogeneous rays like the so-called primary rays of oak. In fact, in the genus *Alnus* species may be found which form a perfect series of transitional steps between alders with non-aggregated uniseriate rays and *Alnus rhombifolia* Nutt., which often possesses large compound rays such as are found in the higher oaks.

Further, EAMES has shown that in the development of seedling oaks a similar series of stages occur. Thus in seedlings of *Quercus alba* L. and *Q. rubra* L., which in the adult possess broad homogeneous rays, the first-formed wood resembles the adult wood of chestnut in possessing non-aggregated uniseriate rays. In the further growth of the young plant, aggregations of rays develop, which by subsequent fusion constitute the large rays of the mature wood.

Thus three lines of evidence, afforded by the study of seedling stages, fossil ancestral forms, and the development of ray structures in living forms, show conclusively that the wood of primitive Fagaceae and Betulaceae was characterized by the entire absence of large medullary rays. With the development of unequal seasonal temperatures, a highly organized storage system for foods became advantageous to plants, and the large rays of modern oaks have been evolved by an aggregation and fusion of numerous uniseriate rays to meet this demand.

With these preliminary statements on the normal and ancestral features of oak wood, we may now turn to a more detailed consideration of the abnormal structures which exist in traumatic oaks. It has been pointed out above that traumatic regions are often the seat of ancestral characters and show a series of stages similar

[8] Relation of the leaf trace to the origin and development of compound rays in the dicotyledons. Annals of Botany. *In ed.*

to embryonic or seedling stages. We should accordingly expect to find in wounded oak wood a reversion to primitive ray structure. That this reversion does occur has been shown conclusively by the examination of numerous areas of wounded oak wood. In fact, in all cases a complete series of transitional stages in the development of compound rays occurred, resembling the series of steps found by EAMES in the development of seedling plants. The wood formed immediately after wounding possesses characteristically only uniseriate rays. In following layers aggregations of the rays develop, with subsequent enlargement of the uniseriate rays, and their subsequent fusion into homogeneous masses or compound rays. During this compounding process, fibers and wood parenchyma included in the fusing mass are transformed into ray parenchyma.

In all cases, in securing material, burls and distorted tissues were carefully avoided and straight-grained traumatic tissue selected.

In fig. 1 may be seen a tangential section of the normal adult wood of *Quercus nigra* L. The so-called primary and secondary rays are characteristically developed; the former consists of a homogeneous mass of ray parenchyma. In contrast to this the traumatic wood of the same species may be seen in fig. 2. The large ray is seen to consist of a compounding mass of smaller rays.

Figs. 3 and 4 illustrate the normal and traumatic condition in *Quercus virginiana* Mill., the important live oak of the southern United States. As may be seen, in this species the normal adult wood is characterized by an imperfectly compounded ray. Numerous included fibers and wood parenchyma cells, evidences of fusion, are usually present. Fig. 4 illustrates the reversion of the wood in the vicinity of the wound to the non-aggregated uniseriate condition.

In figs. 5 and 6 are shown sections of the normal and the traumatic wood of *Quercus densiflora* Hook. and Arn., a live oak whose normal adult wood is characterized by large rays in which the process of compounding is clearly shown. The wounded wood of the species reverts to a more primitive type of compounding, as may be seen in fig. 6.

Figs. 7–10 illustrate the normal and traumatic wood of the well known *Quercus alba*, a deciduous oak with highly specialized ray structure. Figs. 8 and 10, tangential and transverse sections respectively of the traumatic wood, show that this species also reverts to ancestral type of ray structures.

This reversion to ancestral conditions has been found by the writer in woody tissues subsequent to severe injury. Slight injuries, on the other hand, particularly in oaks with highly specialized ray structure, often produce no morphological effect upon the wood. In a limited number of cases very slight wounds have produced a stimulation of the compounding tendency or acceleration of development rather than a reversion to ancestral structures. In fig. 11 may be seen a cross-section of *Alnus* sp. The lower portion of the figure shows none of the so-called false rays, but in the upper half numerous rays have developed abruptly outside a zone indicating slight injury. Fig. 12 shows a similar phenomenon in the young stem of *Quercus densiflora*. In the lower half may be seen normal seedling wood in which only uniseriate rays occur. Starting from a zone of slight injury in the middle of the section, a compound ray has suddenly appeared in the upper portion of the figure. From this we see that very slight injuries produce an acceleration in the formation of compound rays.

SUMMARY AND CONCLUSIONS

1. The phylogenetic importance of traumatic areas as the seat of reversion to primitive structures is well illustrated by the specimens of wounded oak wood which have been examined by the writer.

2. In traumatic wood progressive stages are found which are similar to the stages of recapitulation found in the seedling, and equivalents to the condition found in adult miocene oaks.

3. Woody tissues in the immediate vicinity of a severe wound show only non-aggregated uniseriate or small rays. In subsequently formed tissues the gradual building up of the compound ray may be traced in a consecutive series of steps to the normal homogeneous large ray of the adult wood.

4. On the basis of traumatic and developmental as well as paleo-

botanical evidence, the large homogeneous masses of ray parenchyma, or the so-called primary rays of oaks with deciduous foliage, appear to have been built up by an aggregation and fusion of numerous uniseriate rays.

5. Traumatic reversions are confined to regions which have been severely injured. Occasionally areas where the traumatic effect has been slight show an acceleration of the compounding process instead of a reversion to ancestral stages.

6. The so-called primary ray is seen to have originated from an aggregation and fusion of secondary rays, and to be in no way related to inclusions of fundamental tissue between the primary fibrovascular bundles. From this phylogenetic relation of the two sorts of medullary rays it seems that the term primary is inadmissible entirely for the large rays of oak, and that the term *compound* might be advantageously substituted.

In conclusion I wish to express my sincere thanks to Mr. G. B. SUDWORTH, dendrologist of the U.S. Forest Service, for material of *Alnus rhombifolia*. I am also much indebted to Professor E. C. JEFFREY for suggestions and advice, and to Mr. A. J. EAMES for material of several wounded oaks.

HARVARD UNIVERSITY
CAMBRIDGE, MASS.

EXPLANATION OF PLATES XI AND XII

PLATE XI

FIG. 1.—*Quercus nigra:* tangential section of the normal adult wood, showing the so-called primary and secondary rays; the former are seen to consist of large masses of homogeneous ray parenchyma; ×120.

FIG. 2.—*Quercus nigra:* tangential section of the traumatic wood, showing compounding mass of small rays; ×120.

FIG. 3.—*Quercus virginiana:* tangential section of the normal adult wood, showing strong evidences of a compounding process; inclusions of fibers and wood parenchyma cells occur conspicuously; ×120.

FIG. 4.—*Quercus virginiana:* tangential section of the traumatic wood, showing uniseriate non-aggregated rays in the immediate vicinity of a severe wound; ×120.

FIG. 5.—*Quercus densiflora:* tangential section of the normal adult wood, showing aggregating and fusing mass of small rays; ×60.

FIG. 6.—*Quercus densiflora:* tangential section of the traumatic wood, showing aggregation of uniseriate and biseriate rays; ×120.

PLATE XII

FIG. 7.—*Quercus alba:* tangential section of the normal adult wood, showing highly organized broad homogeneous ray; ×120.

FIG. 8.—*Quercus alba:* tangential section of the traumatic wood, showing the aggregation and fusion of triseriate and biseriate rays; these rays have been produced by the enlargement or growth in diameter of uniseriate rays; ×120.

FIG. 9.—*Quercus alba:* transverse section of the normal adult wood, showing the highly organized type of ray; ×120.

FIG. 10.—*Quercus alba:* transverse section of the traumatic wood, showing aggregation of uniseriate, biseriate, and triseriate rays; ×120.

FIG. 11.—*Alnus* sp.: transverse section of very slightly injured wood; compounding rays are absent from the lower half of the section; starting abruptly from a line of slightly injured tissue which crosses the middle of the section, numerous rays extend outward to the exterior of the stem; ×40.

FIG. 12.—*Quercus densiflora:* transverse section of very slightly injured wood; the lower half of the section possesses only uniseriate rays, but starting from the middle of the section a compounding ray has originated from a slight injury to the wood; ×60.

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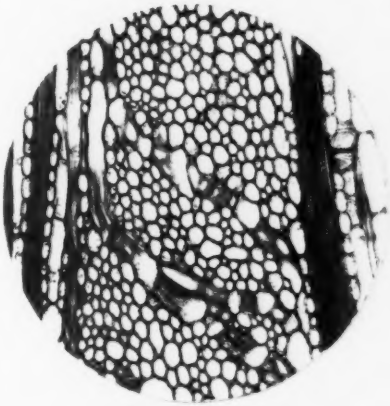

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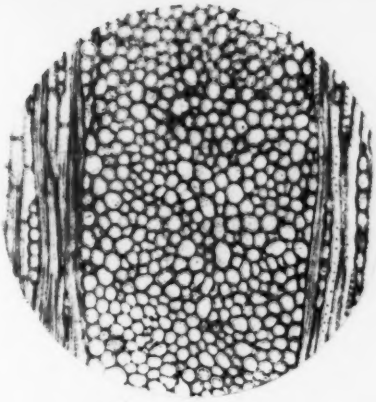
BAILEY on OAK WOODS



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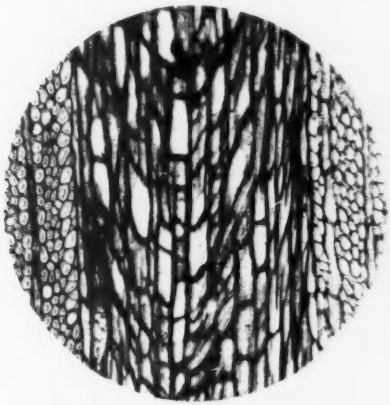

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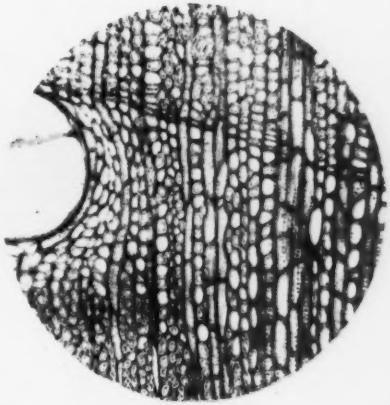

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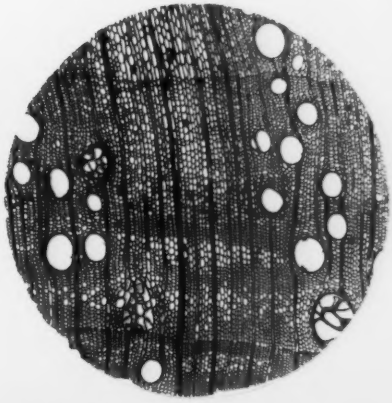


12

BAILEY on OAK WOODS

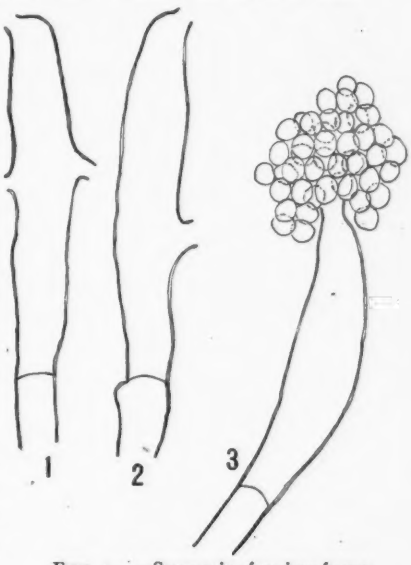
BRIEFER ARTICLES

ANOTHER NEW ACHLYA

(WITH EIGHT FIGURES)

In the fall of 1909 a species of *Achlya* that was found to be new appeared in cultures from pools around Chapel Hill, N.C. It was separated from other forms and has now been kept under observation in pure cultures for nearly a year. It adds one more to the *Racemosa* group proposed by me in 1908.[1] The species may be described as follows:

Achlya caroliniana, sp. nov.—Hyphae rather stout, about 48 μ at the base and 20 μ near the tip, in strong cultures reaching a length of 1.5 cm. Zoosporangia irregularly cylindric, about 20–30 μ in diameter, often discharging by several openings. Oogonia abundant, spherical, smooth, and unpitted; terminating short, slender branches, which are racemosely borne on the strong main hyphae. Oogonial branches generally simple, but often giving off one or two branches near the base which also terminate in oogonia, and, as a rule, are curved downward. Oospores generally 1 or 2, often 3, and very rarely 4 or 6 (8 were seen twice). They are centric, with a diameter varying from 18.5 to 26 μ, averaging about 22 μ. Antheridia absent, but hypogynous antheridial tubes often appear through the basal partition exactly as in *Achlya hypogyna* Coker.



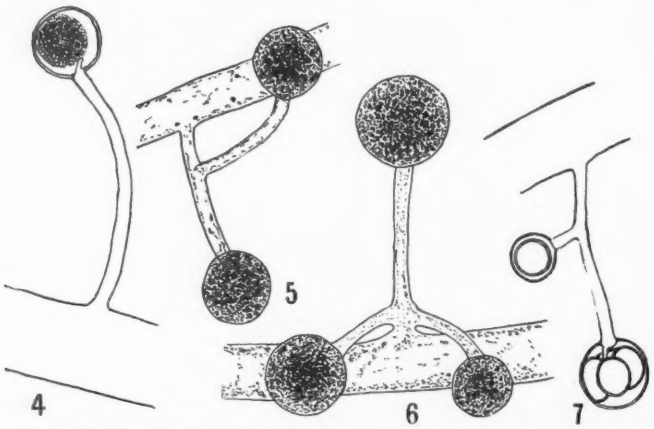
FIGS. 1–3.—Sporangia of various forms; all ×335.

Typical zoosporangia are shown in figs. 1–3. In cultures that have become somewhat foul, the spores may be fully formed, but not discharged. In several such cases the spores

[1] A new species of Achlya. BOT. GAZETTE 45:194, 195. 1908.

were seen sprouting and sending their tubes through the sporangium wall, as is normally the case in *Alpanes*.

Figs. 4–7 represent the normal arrangement of the oogonia; the hypogynal tube will be noticed in fig. 4. In countings from my cultures,



FIGS. 4–7.—Fig. 4, simple oogonial branch terminating in an oogonium; fig. 5, oogonial filament with one branch; fig. 6, same with two branches; fig. 7, a branched oogonial filament with terminal oogonium containing four oospores; all ×335.

this tube was present only in about one-sixth of the oogonia, but it appears in all cultures and is one of the most distinctive characters of the species. The appearance of an antheridial tube, not from an antheridium, but from the vegetative coenocyte, is a most singular occurrence, and would seem to be a degenerate condition induced by the suppression of fertilization. I could find no evidence of fertilization even in cases where a tube was found. In not a single case was an antheridium seen below the oogonium.

FIG. 8.—Exceptional oogonium with two projections on surface; ×335.

The arrangement shown in fig. 6, suggesting the three balls of a pawnbroker's shop, occurs so often and is so striking as to be one of the best diagnostic characters of the species. The lower branches are typically recurved (figs. 5, 6), but not always (fig. 7).

Out of many thousands of oogonia seen, a very few had one or two short rounded outgrowths from

the surface (fig. 8) like those that are characteristic of *A. hypogyna*. In only two cases were intercalary oogonia seen.

In old cultures the protoplasm becomes condensed and segregated into certain restricted areas of the hyphae to form resting fragments, which, though not of definite shape, may be regarded as chlamydospores.

In the *Racemosa* group, as mentioned above, there may now be included *A. racemosa*, *A. racemosa* var. *stelligera*, *A. hypogyna*, and *A. caroliniana*. The group may be defined as follows:

Oogonia terminating short branches, racemosely arranged. Oospores few, generally one or two. Antheridia absent, or of suboogonial origin.—W. C. COKER, *Chapel Hill, N.C.*

SOME NEW SAPROPHYTIC FUNGI OF THE MIDDLE ROCKY MOUNTAIN REGION

Until a year ago (June 1909) the saprophytic fungi of the Rocky Mountain region included within Wyoming had remained practically untouched. It was with great interest, therefore, that the writer began the task of making a collection of these fungi under the kindly suggestion and help of Professor AVEN NELSON. The particular region studied includes the whole of the Medicine Bow National Forest, together with the vast extent of the Laramie Plains. The timber in the forest is chiefly lodgepole pine, Englemann spruce, Douglas fir, and balsam, with dense growths of aspen on the boundaries. In many places the timber is very dense, in consequence of which the humus formed of the needles is very thick; the soil in the open timber also is very rich. The whole region is well watered by the melting snows and by the numerous mountain streams and creeks, resulting in very favorable conditions for the growth of the fleshy fungi. The great difference in the altitude, which ranges from 2130 to 3900 meters, further aids in the formation of many varying conditions, thus giving not only richness in specimens but a wealth of species as well.

In the very precursory examination of the region, the writer was astonished at the great quantity and variety of forms. The further collections, which it is expected will be made, will no doubt extend the list greatly. This list, as finally worked out, will be published as a whole, but for the present the following apparently new species only are presented.

Catathelasma, gen. nov.—Pileus somewhat fleshy, convex, then expanded: lamellae very decurrent, somewhat unequal, with acute edges:

stipe furnished with a ring and of the same substance as the pileus: volva large, white, with a thick margin: spores white.

The ring and volva, together with the very decided decurrent gills (upon which character the generic name is based), are telling characteristics of this genus of the Leucosporae.

C. evanescens, sp. nov.—Pileus 13 cm. broad, white, deep cream in center, broadly convex to nearly plane, smooth, damp, broadly elliptical in outline; margin entire: flesh whitish, compact, thick in center, thinner near margin: lamellae very decurrent, short ones intermixed with long ones, white, 2–3 cm. wide near margin of pileus, becoming narrowed near and on stipe, subdistant, edges acute: stipe very short, thick, 1 cm. long, 4 cm. thick, fleshy, hollow, smooth, white; annulus delicate, evanescent, situated on stipe just below gills: volva large, white, smooth, opening around top leaving a thick even white margin, persistent and closely embracing base of stipe: base large, white, bulbous: spores white, smooth, elliptic to fusiform, 14–17.5×3–5 μ.—Whole plant when dried becomes a rich ochre with reddish tinge.

Habitat: Open balsam and spruce woods, occurring singly in sod on thick humus; Brooklyn Lake, Wyoming, Snowy Range, alt. 3500 meters, September 8, 1909, no. 88.

Clitocybe pruinosa, sp. nov.—Pileus 3.5 cm. wide, plano-convex to slightly depressed, rich reddish brown over salmon, paler at margin, dry, smooth, shining: margin turned down and entire: flesh compact, white, tinged with color of cap: lamellae thin, narrowing behind, salmon yellow, close, very decurrent, becoming somewhat powdered with numerous white spores: stipe fleshy, 5 cm. long, 1 cm. wide, concolorous but lighter than cap, hollow, smooth: spores white, spiny, globose, 7–10.5 μ.

Habitat: Pine humus, open pine woods; Foxpark, Wyoming, August 14, 1909, no. 83.

COLLYBIA MACULATA **moschata,** var. nov.—Pileus fleshy, firm, 6 cm. wide, convex to nearly plane, white, glabrous, shining, becoming tinged or stained with pinkish red blotches, disk sometimes broken up into large polygonal plates; margin turned down and even; flesh white, compact, tinged with pink just beneath the surface: lamellae whitish, in one specimen a faint pink tinge, adnexed to nearly free: stipe stout, firm: 3 cm. long, 2 cm. wide, swollen in middle, stuffed, becoming hollow, curved, narrowed at base, striate, slightly roughened by broken fibers, spores white, smooth, sometimes with a slight point at one end, 7×4 μ.—It has a strong, almost overpowering odor of musk.

Habitat: On side of dead lodgepole pine log, clustered; Foxpark, Wyoming, alt. 2900 meters, August 13, 1909, no. 79.

Entoloma viridans, sp. nov.—Pileus 3.5–5.5 cm. broad, fleshy, broadly convex, hygrophanous when moist, gray, margin tinged with rose pink and disk becoming dull green, or the coloring may be reversed, the disk rose pink and margin a dull green, when dry the whole plant becomes silky shining: flesh white, becoming dull when dry: margin turned down, entire, smooth: lamellae all even, light pinkish yellow, becoming a salmon pink color, 2 mm. broad, slightly sinuate, adnate then separating, interspaces venose: stipe fleshy, white, pruinate, hollow, round, quite bulbous at base, attenuating upward, 4.5 cm. long, 1.5 cm. wide: spores coarsely warted, pink, 7×10 μ.

Habitat: Damp humus; Brooklyn Lake, Wyoming, alt. 3500 meters, bank of Nash's Fork, September 3, 1909, no. 119.

Gloeophyllum ferrugineum, sp. nov.—Pileus hard, corky to woody, oblong-dimidiate to flabelliform, 1–2×2–12×1–1.5 cm.; surface azonate, strigose-tomentose, scrupose, dark ferruginous to umbrinous; margin rather thick, sterile, tomentose, bright ferruginous: context corky, homogeneous, bright ferruginous, indistinctly zoned, about 7 mm. thick; tubes lamelloid, quite decurrent, tomentose, ferruginous but paler than margin of pileus, light grayish within, 1–2 mm. broad, 2–5 mm. deep; edges somewhat thin, tomentose, undulate; tubes lamelloid from the first: spores globose-ellipsoid, smooth, hyaline, 10–14×7 μ.

Habitat: On dead lodgepole pine and aspen; Cooper Creek, Wyoming, alt. 2800 meters, June 22, 1909, no. 11.

Clavaria truncata, sp. nov.—Pileate tops bright red, shading into reddish orange at top of stipe to dull flesh color at its base: ends truncate, convex to plane to somewhat concave, 0.5–3 cm. broad, smooth: whole plant to within a few centimeters of base of stipe covered with a white bloom, persisting in dried specimens: flesh creamy, spongy: stipe longitudinally grooved to base, 3–10 cm. long: spores white, 14×7 μ.

Habitat: Humus soil under balsam and spruce trees; gregarious and cespitose, 4–6 in a group; Foxpark, alt. 2900 meters, August 8, 1909, no. 66.

A plant similar to this is described by FRIES as *Craterellus pistillaris*, and by others as possibly a variety of *Clavaria pistillaris*, but in a collection of twenty specimens found in entirely different localities not one out of the number was found to have either the color or the form of typical *Clavaria pistillaris*.

RUTH HARRISON LOVEJOY, *University of Wyoming, Laramie.*

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RUTH HARRISON LOVEJOY, *University of Wyoming, Laramie.*

CURRENT LITERATURE

BOOK REVIEWS

The root-fungi of orchids

BURGEFF[1] has brought together the extended results of his own research and those of other students upon the root-fungi of orchids. The volume contains a comprehensive citation of literature, several tables summarizing results of experiments, and discussions of the theory of the mycorhiza question. By way of introduction, BURGEFF defines his use of the word symbiosis as that relation of two symbionts in which one aids the other in any way, if only to make existence possible under conditions otherwise impossible. After union, the two organisms form a new organism, a unit, which takes up the struggle for existence under new conditions, each being a body member. Such is claimed to be the condition of the orchids and their root-fungi. The two sections of the work are as follows:

1. *The study of the fungus independent of the plant.*—On a culture medium of agar and rain water with a slight trace of starch, 29 root-fungi, aseptically obtained from native and tropical orchids, were grown (holosaprophytic ones were unsuccessful). Such species of *Orcheomyces*, as the author chooses to call the fungi for convenience, are described in detail as to their structure and behavior in the culture. For the first time a study of their enzymes has been made, and the endophytes were grouped accordingly on the basis of their biological relations to the orchids. In general they have thin-walled, regularly septate mycelia; the hyphae are sharply differentiated into *Langhyphen* that branch little and show unlimited growth in one direction, and *Kurzhyphen* that are of smaller caliber and arise at regular intervals and whose cells under certain conditions are transformed into spores (*Sporenträger*) or absorptive hyphae (*Sanghyphen*). In old age spores and hyphae contain a fatty oil. Chains of hyaline or slightly colored spores may unite into loose clusters or closer sclerotia-like groups. All fungi fuse or anastomose in some manner. The hyphal cells contain two to ten nuclei, but the spores contain only two nuclei. Spiral knots initiated in cultures by the surface tension of a drop of water at the tip of the hypha are comparable to those in the root cells developed in response to the pressure of the resisting plasma membrane to the penetration of the hypha. No sexual reproduction was observed.

[1] BURGEFF, HANS, Die Wurzelpilze der Orchideen; ihre Kultur und ihr Leben in der Pflanze. 8vo. pp. 207. *pls.* 3. *figs.* 38. Jena: Gustav Fischer. 1909.

———, Zur Biologie der Orchideen Mycorhiza. pp. 66. Inaug. Diss. Jena: Gustav Fischer. 1909.

Of the carbohydrate culture media, starch, maltose, and saccharose were best; glucose and dextrin next; and glycerin poorest. Correspondingly, all fungi possessed diastase and emulsin; some invertase and maltase; some aesculin; one tyrosinase; and only one cytase. In humus decoctions all grew well.

The endophytes cannot assimilate free nitrogen. They belong to BENNECKE'S category of "Ammon-nitrit-nitratpilze," and grow luxuriantly, forming spores on ammonium salts, ammonium nitrate holding first place. Organic N compounds were varyingly well assimilated. Peptone produced splendid growth, and salep furnished sufficient N for all to grow. All fungi possess proteolytic enzymes.

The production of acid in assimilation is slight, and in general, in media containing asparagin, peptone, or urea, is in proportion to the intensity of the growth. Orchid fungi require to a high degree atmospheric oxygen, dying in long-continued anaerobic cultures. The formation of spores and spore sclerotia depends upon the concentration of the medium, its exhaustion, and the amount of assimilation products present. Salep always stimulated spore-formation, as did increased transpiration.

2. *The study of the plant and the fungus.*—For the biological relations of the plant and the fungus, BURGEFF chooses the terrestrial orchid *Epidendrum* (*dichromum?*) and the hybrid epiphyte *Laelio-Cattleya*. Without a fungus, seeds of *Epidendrum*, on a culture medium of rain water, 2 per cent salep, and 1.5 per cent agar, did not germinate. With ten different fungi they germinated within 25 days. The embryo did not become green until infected. Thinned nutritive agar cultures with fungi produced stouter plants than the rain water cultures. The stages of development and limits of the fungus agree with the *Cypripedium* type of development described by BERNARD. Infection takes place through the suspensor at first, and later through the root hairs, passing by means of the *Durchlasszellen* into the cortex. The hyphae of the sub-epidermal layer (*Pilzwirtzellschicht*) are never digested, but *Eiweisshyphen* appear in the digestive layer beneath. The cytological facts agree with the phenomena of digestion, where the remains (a clump) are surrounded by a cellulose layer (*Haut*), and the nucleus assumes the resting stage, ready to digest new hyphae. Clumps may become several-layered.

BURGEFF found that the seeds of *Laelio-Cattleya*, wettable only after three or four days, could germinate, become green, and attain considerable differentiation (stomata at apex, rhizoids at base, leaf primordia) in three or four months. A resting period of a year is necessary before growth continues, for which also a fungus is required. Just before infection, the oil in reserve in the cells near the suspensor is transformed to starch, which disappears, however, as soon as the fungus penetrates the cells. Both embryo and fungus show evidence of growth, the latter by the formation of *Eiweisshyphen* (homologous with spores and hyphal knots).

Testing the possibility of saprophytic germination in *Laelio-Cattleya*,

BURGEFF obtained its development, in 0.33 per cent cane sugar with mineral salts on agar, in the dark, to the differentiation of papillae, and it lived ten months. Further development either in light or dark required the fungus. While in the light the orchid developed normally, in the dark it elongated and resembled the *Epidendrum* which grew in the weaker concentration of salts. BURGEFF concludes that physiologically the behavior of the fungus is alike in the germination of the epiphyte and the terrestrial orchid, and that the appearance of chlorophyll in the epiphyte is an adaptation to its life in the light.

Seedlings with the fungus in absence of CO_2 in the dark grew, but developed no root, while in the light the growth was normal. Experiments on the physiology of nutrition, where fungus and seedling were grown together, showed the best N sources to be ammonium chlorid and nitrate. Although asparagin was favorable for the fungus in free culture, the plant could not grow in it. In N-free media there was no development. Lactic acid (2 per cent) in mineral salt agar culture caused both plant and fungus to grow well. *Laelio-Cattleya* was found to harbor some fungi (17 tested) unable to stimulate its germination.

BURGEFF devotes 50 pages to the histological processes in the growing plants. These detail the places of entrance, position of the fungi, peculiar features in the plant cell (spores and clumps, *Klumpenbildung*), the emission of hyphae to the substratum, etc. Most of the fungi have mycelial connections with the outside substratum, therefore anatomically there is nothing to prevent ascribing to such hyphae the function of conduction of soluble materials. The author explains the unwettability of the seeds as due to the *Luftbläschen* in the netted testa itself, and to the air between the testa and embryo (comparable to the condition in the lycopod spores). Such unwettability hinders the passage of spores through the soil, contrary to the theory of KOCH and LÜSTNER, but is of advantage in preventing the clinging together of seeds in the capsule, therefore an adaptation to their dissemination by wind. Also because the seeds are chemically attracted to the fungi, the unwettability is an adaptation in terrestrial orchids against too rapid exhaustion of this substance.

BURGEFF agrees with BERNARD in the probable steps of development of the symbiosis by way of parasitism, but would speak of the association not as a "maladie bienfaisante," but as of "einem glücklichen Zusammentreffen verschiedener Umstände." He bases this remark on the following facts: the fungus is harmless, its enzymatic qualities separating it from comparison with parasites with toxic qualities; it is able to kill an unadapted fungus whose penetration it nevertheless allows; its fitness for infection is seen in the *Durchlasszellen* of the embryo. A mutualistic symbiosis demanded by the definition is found in this association, for the orchid has to thank the fungus for its existence, and the fungus is grateful to the orchid for the materials difficult to obtain from the soil which enable it to form spores. As to the materials of exchange between the components, the question is left unanswered; but the idea of conduction of mineral salts is favored, because of the results of the

cultural experiments and because of the detailed morphological and anatomical features of both symbionts. The fungus causes the conversion of starch into sugar by its diastase. Its function results from its enzymatic quality, which, with the solution of carbohydrates in the plant cell, induces the development of the seed, not by bringing soluble materials to the cell, but by transforming substances already there. BURGEFF suggests here the unproven fact of diffusion of the diastatic enzyme out of the fungal hypha through the *Plasmahaut* into the plant cell. This may also occur in the substratum from the emission hyphae. The osmotic relations arising from the sugar solutions could account for the absorption of water, but if nutritive salts are absorbed from the fungi from outside, a rapid change in permeability and adjustment of pressures at just the proper time to seize the salts brought by the fungus must take place.

On the whole, the relations between the plant and the mineral salts of the soil are of striking importance for the origin and maintenance of the orchid symbiosis. Although the structures show a gain in nitrogenous substances, the habitats of orchids, and cultural experiments exclude the possibility of free N-absorption. No anatomical features can prove the absorption of organic carbohydrates; although diastase and emulsin are common to all fungi, material for the action of the former is lacking in the soil, and we are in ignorance concerning the substance in the soil digested by the latter. Any substance taken up by the plant, either through its roots or by means of the fungus, must first be made soluble by the fungus itself, or by its exoenzymes in the substratum.—GRACE L. CLAPP.

MINOR NOTICES

Farm weeds.—The preparation of a scientific manual for the use of the ordinary layman is admittedly a difficult task, but it has been successfully accomplished by CLARK and FLETCHER,[2] whose volume upon farm weeds is the best that has yet appeared upon this subject. The remarkable simplicity without the sacrifice of scientific accurracy is due largely to the splendid ability of the late Dr. JAMES FLETCHER, who thus adds one of the latest of his many valuable contributions to botany and agriculture. More than 200 of the more troublesome weeds of Canada are arranged according to modern botanical classification, with very complete scientific and common synonyms, and briefly but accurately described in non-technical language. Special attention is directed to the characteristics which make the various plants troublesome as weeds, and careful directions are given for the most practicable and successful methods of control and extermination.

The most valuable aid to the recognition of different species is a series of 76 full-page plates, colored with the greatest accuracy. They include

[2] CLARK, GEORGE H., and FLETCHER, JAMES, Farm weeds of Canada. Second edition. 8vo. pp. 192. *pls. 76*. Ottawa: Department of Agriculture, Dominion of Canada. 1909. $1.00 (single copies only, for sale by Superintendent of Stationery, Government Printing Bureau, Ottawa).

representatives, in natural size and also much enlarged, of the seeds of 100 of the most troublesome species. These illustrations are from the water-color sketches of NORMAN CRIDDLE, and will enable the farmer to identify readily most of his plant enemies, either while they are growing in the field or while polluting his seed grain.

The book is well printed and strongly bound, which, together with its other admirable qualities, makes it a valuable addition to the literature of economic botany.—GEO. D. FULLER.

A text-book of pharmacognosy.—A fourth edition of KRAEMER'S *Text-book* has appeared.[3] It is "intended for the use of students of pharmacy, as a reference book for pharmacists, and as a handbook for food and drug analysts." Such a statement indicates that the volume does not fall within the province of a botanist for review, and yet the material presented is of great interest to botanists. Part I (pp. 222) is entitled "Botany," and comprises a presentation of all the great groups, "outer morphology of angiosperms," "inner morphology of the higher plants," "classification of angiosperms yielding vegetable drugs," and "cultivation of medicinal plants." Of course this is botany for the pharmacist, and Dr. KRAEMER is in a position to know what the pharmacist needs. Only the first chapter, dealing with the great groups, really pertains to the non-pharmaceutical botanist. Perhaps it makes no difference to the students concerned, but the very antique flavor of the presentation of the great groups is somewhat surprising to the modern morphologist. Part II (pp. 383) is entitled "Pharmacognosy," and deals first with crude drugs, and then with powdered drugs and foods. Part III (pp. 88) is entitled "Reagents and technique"; and part IV (pp. 38) deals with "Micro-analysis."

The volume is certainly a thesaurus of information for the pharmacist, and doubtless will have great influence upon the progress of pharmacognosy in this country. There is abundant evidence, also, of an immense amount of painstaking labor on the part of the author, who is to be commended for his many years of faithful effort to organize and advance his subject.—J. M. C.

A naturalist in the Bahamas.—Under this title a memorial volume in honor of Dr. JOHN I. NORTHROP has appeared.[4] The botanical papers are as follows: "Flora of New Providence and Andros (Bahama Islands)," by ALICE R. NORTHROP (reprinted from Mem. Torr. Bot. Club **12**:no. 1. 1902); "Plant notes from Temiscouata County, Canada," by JOHN I. and ALICE R. NORTHROP (reprinted from Bull. Torr. Bot. Club **17**:1890); "Notes on the plant distribution of Mt. Washington, N.H.," by JOHN I. and ALICE R. NORTHROP; and

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[3] KRAEMER, HENRY, A text-book of botany and pharmacognosy. pp. viii+888. Philadelphia and London: J. B. Lippincott Company. 1910. $5.00.

[4] A naturalist in the Bahamas. JOHN I. NORTHROP. Oct. 12, 1861—June 25, 1891. A memorial volume edited with a biographical introduction by HENRY FAIRFIELD OSBORN. pp. 281. New York: The Columbia University Press. 1910. $2.50.

"A study of the histology of the stem of the wax plant, *Hoya carnosa* (L.) R. Br.," by JOHN I. NORTHROP.—J. M. C.

NOTES FOR STUDENTS

Prothallia of Lycopodium.—BRUCHMANN[5] has completed the life histories of *L. clavatum*, *L. annotinum*, and *L. Selago*, with an account of the growth of the prothallia from the germination of the spores to the maturing of the sex organs, and with the study of the embryo development of *L. Selago*. Previously the germination of only three species was known, all with a prothallium containing chlorophyll and belonging to the *cernuum* type: *L. salakense*, independent in development and free from a fungus; *L. cernuum;* and *L. inundatum*, dependent for complete development upon an endophytic fungus.

The germination of the spores was secured by sowing them in the forest where they were found. This was done in two ways: (1) by putting spores and species of fresh strobili into flower pots in potting soil (peat, leaf mold, manure, sand) and forest soil and sinking them in the ground; and (2) by mixing spores with forest soil and burying them in holes 10 cm. deep. The germination of *L. Selago* occurred in 3–5 years after sowing; that of *L. clavatum* and *L. annotinum* in 6–7 years. Prothallia bearing mature sex organs appeared first in *L. Selago* 6–8 years after sowing; in *L. clavatum* and *L. annotinum* in 12–15 years. Practically all the spores of a sporangium of *L. Selago* germinated, but only about 5 per cent of those of other species. All three species develop independently a five-celled chlorophyllose prothallium, after which a fungus is necessary to complete the development. *L. clavatum* and *L. annotinum* develop in the same way, while *L. Selago* forms a type by itself.

The first division, an irregular one, cuts off a small lens-shaped cell at the base of the spore. Although containing food substances, it is poor in cytoplasm and never enlarges. BRUCHMANN considers it a rudimentary rhizoidal cell, homologous with the first rhizoid of the true ferns. The second division, occurring after the spore coat bursts, extends an oblique wall from base to apex, bent toward the rhizoidal cell. While in the *clavatum* type this wall divides the prothallium into hemispheres, in the *Selago* type it is sharply bent away from the rhizoidal cell, making the resultant cells unequal. The difference in direction determines the type of prothallium. The basal cell next to the rhizoidal cell never divides. Its sister cell cuts off an inner wedge-shaped cell and an outer apical cell. A fourth wall divides the wedge into an outer peripheral and an inner or central cell. In *L. Selago* the wedge-shaped cell is considered the first segment cut off from the apical cell.

From this point BRUCHMANN divides the growth of the prothallia into three periods, depending upon change in direction and manner of growth.

[5] BRUCHMANN, H., Die Keimung der Sporen und die Entwicklung der Prothallien von *Lycopodium clavatum*, *L. annotinum*, und *L. Selago*. Flora 101:220–267. *figs.* 35. 1910.

L. Selago resembles closely *L. Phlegmaria* in development, while *L. clavatum* and *L. annotinum* are alike. The entrance of the fungus at the peripheral or basal cell stimulates the apical cell to division. It cuts off from its two sides alternately five or seven segments in the *L. clavatum* type, and fewer in *L. Selago*. This closes the first period.

Extensive growth of both the prothallium and the fungus characterizes the second stage. Rapid radial growth at the apex results in a pear-shaped prothallium. The fungus in the two lycopod types of prothallium represents two species. In *L. clavatum* it forms a peripheral digestive mantle surrounding the central mass of storage cells. Limited from the central cells by a palisade layer, it becomes entirely intercellular. The fungus of *L. Selago* resembles in habit that of *L. Phlegmaria* and fills the entire prothallium posterior to the apical region except the epidermis. The sister cell of a rhizoid, infected by a branch of the mycelium from the hypodermis, serves as an "Expeditionszelle." From it the hypha passes out to the substratum, spraying out into fine branches. To this cell BRUCHMANN attributes the function of chemically attracting the fungus by its enzymes.

The third period has to do with the changes in the apical region. Marginal meristematic cells in *L. clavatum* surround the axial conductive cells, coextensive with the former storage cells. Reproductive organs develop on the margin, antheridia preceding archegonia. Such prothallia may live twenty years. During this period the fungus forms spores. In *L. Selago* the attempt to gain dorsiventrality causes extensive elongation of the prothallium, which at the soil surface develops chlorophyll. The apical growth becomes marginal, the central tissue acting as a storage region. The outer layers on one side develop paraphyses and sex organs; on the other, vegetative cells containing the fungus, which always remains intracellular.

The embryo-development of *L. Selago* agrees in detail with that of *L. Phlegmaria*. The root appears last, later than in *L. clavatum* and *L. annotinum*. The foot is smaller than that of *L. clavatum* and of *L. annotinum*, but less papillate than that of *L. Phlegmaria*. Its continued growth upward bursts the prothallium, whereupon it reaches the light and becomes green.—GRACE L. CLAPP.

Variation in timothy.—An important contribution to the subject of secular variation has been made by CLARK,[6] who has studied the variation in height, weight of forage produced, earliness of bloom, and duration of the period of bloom in timothy (*Phleum pratense*). Data were secured during three successive years on 3505 plants representing 163 pedigrees derived from 22 different states of the United States. As there can be no doubt that timothy, like many other plants which have been studied, consists of a number of distinct hereditary forms or biotypes, the extent of variation, which was found to be

[6] CLARK, C. F., Variation and correlation in timothy. Bull. 279, Cornell University. pp. 301–349. *figs. 111–150.* July 1910.

very great in all characters studied, may not be considered as having great significance, since the bringing in of still other pedigrees from other sections would doubtless have increased the range of variability. No perceptible correlation was found between earliness and height of the plants or between duration of bloom and height of plants. There appeared to be a slight negative correlation between the duration of bloom and weight, but this was very slight and possibly not significant. Between weight and height, as might be expected, there was considerable positive correlation, ranging from 0.274 ± 0.011 to 0.718 ± 0.006. By securing data covering three years from the same series of plants, an interesting new relation has been developed, namely, the correlation between the condition of plants in one year as compared with the same plants in succeeding years, and for this correlation the author gives the name "coefficient of place-variation." This measures the extent to which an individual, found to have a given rank with respect to a variable character in one year, may be expected to hold the same rank in succeeding years, and is a very important consideration from the standpoint of the practical breeder. The correlation coefficients found ranged from 0.382 ± 0.010 to 0.585 ± 0.008. The lowest correlation was found in comparisons between non-consecutive years, as when 1905 was compared with 1907. This would naturally be expected, since there are more disturbing factors in two years than in one. These coefficients are considered rather low, and are taken to indicate the importance of comparing individuals during several years as a safe basis for selection in economic breeding, since there are very good chances that an individual observed to be superior in one season may be inferior in succeeding seasons.—GEO. H. SHULL.

Seeds of horseradish.—It is a well known fact that the horseradish (*Cochlearia Armoracia*) is generally sterile, though it produces a great abundance of flowers and not infrequently produces capsules. BRZEZIŃSKI[7] has induced the development of seeds by removing a circle of the bark from the upper portion of the root a short distance below the collum. Plants so treated produced a considerable number of good seeds, and in one year (1908) he secured 1500 seeds. Of 50 seeds sown in 1907, 30 produced plants, most of which succumbed to disease, but 9 of which grew to maturity. From the same (1906) crop, 200 seeds planted in 1908 produced only 20 seedlings, thus apparently indicating the rapid loss of vitality of the seeds. Only 6 of these reached maturity. These 15 mature seedling plants of the horseradish were not uniform, but were referable to two types, neither of which agreed with the characters of the parent. The ordinary horseradish is intermediate between these two types, though inclining much more strongly to one of them than to the other. Both types of seedlings proved to be somewhat fertile, producing a considerable number of seeds, even without the operation which induced seed-

[7] BRZEZIŃSKI, J., Les graines du raifort et les résultats de leurs semis. Bull. Acad. Sci. Cracovie, Session of July 5, 1909. pp. 392–408. *pls. 12–15.*

production in the parent. Two hypotheses are offered to account for the appearance of these two types among the seedlings: (1) that they are mutations produced as a result of traumatism in accordance with the views of BLARINGHEM; and (2) that the ordinary horseradish is not a natural species as generally believed by taxonomists, but a hybrid, and that the two types of offspring produced from the seeds are partial or complete returns to its parent types. The author inclines to the latter view, and would interpret the sterility of the horseradish as due, not to the accentuated development of fleshy roots, but to a weakening of the sexual development, not infrequently found in hybrids. The reviewer is inclined also to the latter interpretation, and would point out the important bearing the author's method of securing seeds of the horseradish may have in its application to other sterile hybrids. Many experiments have been terminated by the failure of hybrids to produce seeds. It may be that some of these cases will yield to methods of treatment similar to that employed by BRZEZIŃSKI in securing seeds of horseradish.—GEO. H. SHULL.

The ecology of conifers.—STOPES and MOSS have discussed the xerophytism of conifers, and now GROOM[8] considers a number of their ecological features. In the introductory statement three problems are outlined: the cause of their xerophytic foliage and tracheidal wood, the cause of their survival in competition with dicotylous trees, and the cause of the suppression of many forms in past ages. GROOM correctly concludes that not all conifers are xerophytic, in spite of their xerophytic leaf structure, calling attention to VON HÖHNEL'S demonstration of high transpiration in the larch, and to his own experiments which show that coniferous wood, in spite of its tracheidal structure, may conduct water with a rapidity equal to that of a rapidly transpiring dicotylous tree. Attention is called to the fact that the aggregate leaf surface of a coniferous tree may exceed that of a dicotylous tree, because of the immense number of leaves. Indeed, GROOM regards the xerophytic structure of the leaf as a necessity in view of the great amount of exposed surface, and he applies the term "architectural xerophytism" to xerophytism that is dependent upon the organization of the plant rather than upon the direct influence of external factors upon the organs in question. In opposition to STOPES, GROOM regards the tracheidal nature of the wood as a feature of advantage rather than a feature necessitated by heredity, and notes that similar wood tends to occur in various evergreen dicotyls. The extinction of many conifers of past ages is attributed to their imperfect acclimatization, to the fact that they have a great number of insect and fungus enemies, and to their relatively slight power to react advantageously to new conditions. However, their architectural xerophytism makes it possible for them to thrive in nearly all situations, from those that are physically or physiologically dry

[8] GROOM, PERCY, Remarks on the oecology of Coniferae. Annals of Botany 24:241–269. 1910.

to those that are sufficiently humid to permit the development of luxuriant mesophytic forests. GROOM'S paper is most suggestive, and adds considerably to our knowledge concerning the difficult problem of coniferous xerophytism.—HENRY C. COWLES.

Nutrition of the embryo in Labiatae.—BILLINGS[9] has investigated the nutritive mechanism associated with the embryo sac of certain Labiatae, a subject that deserves more attention from morphologists. The ordinary sac which is oval or elliptical in longitudinal section, and which encroaches uniformly upon the surrounding tissues, has come to be regarded as the more or less fixed "type" of angiospermous sac. Among the Sympetalae especially, however, a much more complex nutritive mechanism has begun to be uncovered, including special digestive layers and special absorptive regions of the sac, the latter usually taking the expression of tubular haustorial extensions. BILLINGS investigated 15 species of Labiatae, representing 14 of the most representative genera. The results were uniform enough and differed enough from other sympetalous groups investigated to indicate that such structures may be of taxonomic and even of phylogenetic value. For example, the Scrophulariaceae previously described usually have a well developed digestive layer ("tapetum"), in addition to haustorial extensions of various kinds; but the Labiatae lack the special digestive layer. There are three features common to the species studied, and possibly to the whole family, to which the author calls attention: the micropylar haustorium (more or less extensively developed), the much-elongated suspensor, and the antipodal canal or process. *Salvia* is an exception to this statement, for it has a short suspensor and no micropylar haustorium; and the two species investigated "are unique in having two haustorial outgrowths, one coenocytic and one composed of ordinary endosperm tissue" (these haustoria are in addition to the well developed antipodal canal). The author thinks that such variations from the general conditions as are shown by *Salvia* "suggest a taxonomic rearrangement."—J. M. C.

Correlation in oats.—WALDRON[10] has compared the height of culm, length of head, number of grains per head, and average weight of grains in a variety of oats growing at Dickinson, North Dakota. The examination of 1000 plants discovered decided negative correlations (-0.595 ± 0.013, -0.511 ± 0.015, and -0.404 ± 0.017) between the weight of grains and number of grains per head, weight of grains and length of head, and between weight of grains and length of culm. He reaches the conclusion that in selecting the heaviest grains in this variety, the breeder selects plants somewhat below the

[9] BILLINGS, F. H., The nutrition of the embryo sac and embryo in certain Labiatae. Kansas Univ. Bull. 5:67–83. *pls. 11–14.* 1909.

[10] WALDRON, L. R., A suggestion regarding heavy and light seed-grain. Amer. Nat. 44:48–56. 1910.

average height, with shorter heads and fewer grains, thus emphasizing the importance of selecting the superior plants instead of the superior individual grains. As this variety of oats was undoubtedly a mixture of several distinct biotypes, it does not follow that the same mathematical results would be found in other varieties composed of different mixtures. The variety with which WALDRON worked may have contained a short-headed, short-culmed, heavy-grained biotype. In some other mixture the heavy-grained biotype might have longer culms, longer heads, and more numerous grains, and it would then give a positive correlation where WALDRON found a negative correlation, but this does not lessen the importance of the conclusion reached that the individual plant and not the individual grain is the proper unit of selection.—GEO. H. SHULL.

Anatomy of the seedling of Trapa.—A short paper by QUEVA[11] on the curious seedling of *Trapa natans* recalls the case of "caulicle" vs. "radicle," the question of the importance of the root as a primarily essential part of a seed plant. The author confirms the observations of previous investigators concerning the marked inequality of the cotyledons, the negative geotropism of the caulicle (which he prefers to call the hypocotyledonary axis), and the presence of internal phoem in the stem and leaves. His own investigation has resulted in the discovery of this internal phloem in the hypocotyledonary axis and in the petiole of the cotyledon. Although he finds in the very tip of the hypocotyledonary axis a vascular condition which is peculiarly root-like (two xylem points alternating with two small groups of phloem), yet he thinks it is not root, because (1) there is no rotation of the strands in successive levels from the tip of the organ to the cotyledonary node; (2) the xylem points are too near the periphery of the cylinder to look like root poles; and (3) the whole organ is covered by epidermis, except at the spot where the suspensor was attached. The growth of the caulicle, or hypocotyledonary axis, is limited; the roots strike out from its side, their vascular strands being inserted on certain metaxylem elements discernible in cross-section on one side of the vascular cylinder.—SISTER HELEN ANGELA.

Sporophylls of Selaginella.—SYKES and STILES[12] have made a very interesting study of the sporophylls of *Selaginella*, finding an amount of variation and a degree of complexity that have not attracted attention heretofore. A few of the more representative species are described and the different forms of the sporophyll are pointed out as "special adaptations for the secure protection of the sporangia." In many sporophylls there is a well developed air cavity in the base, and the authors suggest "that they recall the mucilage

[11] QUEVA, C., Observations anatomiques sur le *Trapa natans* L. Compt. Rend. Assoc. Fran. Av. Sci. 1909. Congrès de Lille, pp. 512–517. *figs. 2.* 1909.

[12] SYKES, M. G., and STILES, W., The cone of the genus *Selaginella*. Annals of Botany **24**:523–536. *pl. 41.* 1910.

cavities of *Lycopodium* and the parichnos of fossil genera." In some cases the sporophylls are provided with more or less conspicuous dorsal outgrowths, which have been noted heretofore only in a casual way, but not definitely described. Four types of sporophyll are described: (1) with well developed dorsal flap extending freely downward and protecting the young sporangium immediately below it (as *S. rupestris*); (2) with no dorsal flap, the sporophyll being flat and the sporangium exposed (as *S. spinosa*); (3) with a well developed dorsal projection which is not free but decurrent (as *S. helvetica*); and (4) a series in which the dorsal outgrowth is gradually reduced and lost, each sporophyll more and more completely infolding the sporangium below (as *S. flabellata* to *S. apus*).—J. M. C.

Morphology of Callitris.—SAXTON,[13] in continuing his studies of gymnosperms, has given an account of *Callitris*, an Australasian genus of about a dozen species. The one chiefly studied was *C. verrucosa*, but the results doubtless apply to the genus as a whole, since the species are very closely allied. The sporophylls are in alternating whorls of three, each microsporophyll bearing three sporangia, and each of the upper megasporophylls bearing about 15 ovules, the six sporophylls of the ovulate strobilus producing about 60 ovules. The cells of the mature female gametophyte are all binucleate or multinucleate. The archegonia occur in a single group of about 20, never at the apex of the gametophyte, but along the inner side of the pollen tube near its apex. If two pollen tubes are present, two such groups are organized. The proembryo completely fills the archegonium, the arrangement of cells being variable. More than one embryo is formed from a proembryo, and the first two walls are longitudinal, the mature embryo being dicotyledonous. The claim is well substantiated that *Callitris* and *Widdringtonia* are two distinct genera, but that they should constitute a separate tribe (Callitrineae) coordinate with Cupressineae is not so clear.—J. M. C.

Structure of Mitrospermum.—Mrs. ARBER[14] has investigated the structure of the platyspermous seed described by WILLIAMSON in 1877 as *Cardiocarpon compressum*, and occurring in the British Lower Coal-measures. The outer fleshy (forming the wing-like extension), stony, and inner fleshy layers are recognized and described. Two opposite vascular strands arise from the expanded bundle beneath the nucellus and traverse the outer fleshy layer in the principal plane of the seed, probably continuing almost the whole length of the seed. The nucellus seems to have been entirely free from the integument, and in one seed a tissue within the embryo sac was observed, consisting of "irregular roundish cells," which of course represent the female gametophyte. The

[13] SAXTON, W. T., Contributions to the life history of *Callitris*. Annals of Botany **24**:557–569. *pls. 45, 46.* 1910.

[14] ARBER, AGNES, On the structure of the paleozoic seed *Mitrospermum compressum* (Will.). Annals of Botany **24**:491–509. *pls. 37–39. figs. 2.* 1910.

conclusion is reached that the seed deserves to be removed from *Cardiocarpon*, chiefly on account of its vascular structure, and therefore a new genus *Mitrospermum* is proposed. Whether the seed belongs to *Cordaites* or not was not determined, for the platysperm character can no longer be used as an indication of that group. Sections of unattached seeds must continue to be made, but there is far greater need of sections of attached seeds, for these will probably solve the puzzling embryo situation attributed to paleozoic seeds.—J. M. C.

Phototropism.—NORDHAUSEN[15] offers more evidence against the lens theory of phototropic perception. He finds that leaves of *Begonia* with killed epidermis assume the normal light position, the palisade cells being the perceptive organs. He says that "the epidermis as well as its papillose character are not necessary for light perception." He finds a great difference between the sensitiveness of the two halves of the leaves of *Tropaeolum*, which renders them unsuitable for comparing the effect of light on the wet and dry halves. This plant and method have furnished HABERLANDT with his best evidences for the lens theory. After offering this significant evidence against the theory, he states that HABERLANDT's reply to his former criticism has not rendered that criticism any less applicable. He also holds that the evidence offered in HABERLANDT's later papers is not of a sufficiently critical nature to give the theory any support.—WILLIAM CROCKER.

Carbon dioxid as a fertilizer.—A Berlin company has placed a product on the market known as "Germanol," which consists of an earthy mixture containing about 18 per cent calcinated soda. The company attributes the virtue of this mixture to an increased porosity of the soil following an increase in the proportion of carbon dioxid. MITSCHERLICH,[16] however, is of the opinion that if such a mixture has any value it must be attributed to the action of the carbon dioxid in increasing the solubility of various difficultly soluble soil substances. His comprehensive tests show that increasing the carbon dioxid content of the soil does not result in an increase of plant product; that there is always sufficient carbon dioxid in the soil to render mineral food available; that an increase in the carbon dioxid in the soil does increase the solubility of difficultly soluble substances, but that such increase is superfluous so far as any advantage to the plant is concerned.—RAYMOND H. POND.

Rhizophore of Selaginella.—WORSDELL[17] has used an investigation of the rhizophore of *Selaginella* as the basis of a discussion of the ultimate morpho-

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[15] NORDHAUSEN, M., Ueber die Perzeption der Lichtsichtung durch die Blattspreite. Zeitschr. Bot. **2**:465–506. 1910.

[16] MITSCHERLICH, EILHARD ALFRED, Ein Beitrag zur Kohlensäuredüngung. Landwirtsch. Jahrb. **39**:157–166. 1910.

[17] WORSDELL, W. C., The rhizophore of *Selaginella*. New Phytol. **9**:242–253. *figs. 2*. 1910.

logical categories. He believes that there are "three stereotyped, fixed categories of organs, viz., shoot, leaf, and root," and that there can be no others. "There can be no room in that region of the vegetable kingdom above the level of the homogeneous thalloid types for any organ which is neutral, intermediate, or undifferentiated in character." Incidentally the author furnishes proof, which he says is unequivocal, "that the normal rhizophore has the morphological value of a shoot." This conclusion we are ready to accept, in the absence of any better one, but it is late in the day to defend rigid categories, and to decide what can and what cannot be.—J. M. C.

New genus of flagellates.—GARDNER[18] has described a new genus of flagellates (*Leuvenia*) whose unusual combination of morphological features prevents "any attempt at present to classify it, even to naming the family to which it belongs or in which it has its nearest affinities." The motile, growth, and palmella stages are known. In the growth and mature stages the nuclei and chromatophores are inconstant in number, and in the motile stages contractile vacuoles occur in both anterior and posterior ends, and "pyrenoids, gullet, and stigma are absent." The chromatophores divide by constriction, remain attached for some time by delicate cytoplasmic strands, and are irregular in shape and size.—J. M. C.

Diurnal periodicity in the nitrogen content of leaves.—Investigations hitherto have tended to establish a diurnal periodicity in the nitrogen content of leaves, the fluctuation showing a greater content in the morning than in the evening. CZAPEK, however, in his *Biochemie* states that such investigations should be more comprehensive. With a view to supplying this need, OTTO and KOOPER[19] have made a comprehensive series of analyses which show that even in different stages of development leaves of several different species have a greater nitrogen content in the morning than in the evening. They also found a gradual decrease in the nitrogen content from spring to autumn.—RAYMOND H. POND.

New genera of Chlorophyceae.—GARDNER[20] has described two new genera of green algae growing in association with other marine algae of California. *Endophyton* (*E. ramosum*) is endophytic within the fronds of various species of red algae, and is referred to the Chroolepidae on account of the absence of hair cells, but it has close resemblances to the Chaetophoreae. *Pseudodictyon*

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[18] GARDNER, N. L., *Leuvenia*, a new genus of flagellates. Univ. Calif. Publ. Bot. 4:97–106. *pl. 14.* 1910.

[19] OTTO, DR. R., and KOOPER, W. D., Beiträge zur Abnahme bezw. Rückwanderung der Stickstoffverbindungen aus den Blättern während der Nacht, sowie zur herbstlichen Rückwanderung von Stickstoffverbindungen aus den Blättern. Landwirtsch. Jahrb. 39:167–172. 1910.

[20] GARDNER, N. L., New Chlorophyceae from California. Univ. Calif. Publ. Bot. 3:371–375. *pl. 14.* 1909.

(*P. geniculatum*) occurs among the cells of the cortical layer of species of *Laminaria*, and is also referred to the Chroolepidae. In the same paper a new *Ulvella* (*U. prostrata*) is described, which is epiphytic on *Iridaea laminarioides*.—J. M. C.

Insect galls of Michigan.—COOK[21] has published a list of 59 species of insect galls from Michigan, 31 of them being new to the state. It includes representatives from all the orders of insects that contain gall-makers except the Coleoptera. As there are about 1200 known insect galls in North America, this list of 59 is only a beginning for the state of Michigan.—J. M. C.

Suspensor in Helminthostachys.—LANG[22] has discovered that *Helminthostachys* possesses a massive suspensor closely resembling that of *Botrychium obliquum* described by LYON. Since CAMPBELL has recorded the same structure in *Danaea*, it is becoming evident that a suspensor among pteridophytes is not a peculiarity of the Lycopodiales.—J. M. C.

Two embryo sacs in Fritillaria.—Lechmere[23] has added *Fritillaria* to the short list of monocotyledons that occasionally develop two megaspore mother cells in an ovule. In this case (*F. messanensis*) the two enlarged mother cells are figured as lying side by side, in immediate contact, both nuclei being in the synapsis stage.—J. M. C.

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[21] COOK, MEL T., The insect galls of Michigan. Mich. Geol. and Biol. Survey, Publ. 1, Biol. Ser. 1. pp. 23–33. 1910.

[22] LANG, WILLIAM H., On a suspensor in *Helminthostachya zeylanica*. Annals of Botany **24**:611. 1910.

[23] LECHMERE, A. ECKLEY, Two embryo sac mother cells in the ovule of *Fritillaria*. New Phytol. **9**:257–259. *fig.* 1. 1910.